Comparison of fish assemblage structure and underlying ecological processes, between Cystoseira forests and less structurally complex habitats of North-Western Mediterranean rocky subtidal

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Comparaison de la structure des peuplements de poissons et des processus écologiques sous-jacents, entre les forêts de Cystoseires et des habitats structurellement moins complexes, dans l'Infralittoral rocheux de Méditerranée nord-occidentale

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Résumé

Dans l'Infralittoral rocheux méditerranéen, les algues brunes du genre *Cystoseira* forment des habitats structurellement complexes, dénommés forêts à *Cystoseira*. A cause de certaines activités anthropiques, ces forêts ont déjà disparu dans de nombreuses localités et sont en train de régresser dans d'autres. Elles ont été (sont) généralement remplacées par des habitats structurellement moins complexes de type brousse, gazon ou désert.

Cette thèse a visé à estimer les possibles conséquences pour les poissons de la régression des forêts à *Cystoseira* et à identifier les processus écologiques en cause. Plusieurs approches complémentaires ont été employées : inventaires de macroalgues et de poissons, expériences de prédation et de sélection d'habitats en aquarium, analyses de composions isotopiques et de contenus stomacaux.

Les densités de poissons proie et prédateur étaient plus importantes dans les forêts à *Cystoseira* que dans les habitats structurellement moins complexes. Cela peut résulter, au moins en partie, du rôle "refuge" de *Cystoseira* spp. qui induit (1) une plus faible mortalité des poissons proies et prédateurs dans les forêts, due à une plus grande disponibilité en abris et en nourriture, respectivement, (2) une immigration nette des poissons dans les forêts due à leur préférence pour cet habitat structurellement complexe. De plus, *Cystoseira* spp. pourrait être une importante source de matière organique pour l'écosystème. Ce potentiel rôle "trophique" mérite des études complémentaires.

Ce travail suggère que la régression des forêts à *Cystoseira* est néfaste pour les poissons et souligne donc la nécessité de mieux gérer les activités humaines impactant *Cystoseira* spp..

Mot clés

Ecologie marine ; changement d'habitat ; complexité structurelle de l'habitat ; relations proie-prédateur ; mortalité différentielle ; préférence d'habitat ; source de matière organique ; rôle refuge ; rôle trophique

Title of the PhD thesis: Comparison of fish assemblage structure and underlying ecological processes, between *Cystoseira* forests and less structurally complex habitats of North-Western Mediterranean rocky subtidal

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Abstract

In Mediterranean rocky subtidal, large brown algae belonging to the genus *Cystoseira* form structurally complex habitats, called *Cystoseira* forest. Due to anthropogenic stressors, *Cystoseira* forests disappeared from numerous localities in the Mediterranean Sea and are deteriorating in other localities. *Cystoseira* forests are usually replaced by structurally less complex habitats, such as shrublands, turfs and barrens.

This PhD aimed to assess putative consequences for fish of *Cystoseira* forest degradation, and to identify the underlying ecological processes. Multiple complementary approaches were used: macroalgae and fish field surveys, tank-based predation and habitat-choice experiments, stable isotopes and stomach contents analyses.

Densities of prey and predatory fish were higher in *Cystoseira* forests compared to structurally less complex habitats. This may be due to the shelter role of *Cystoseira* spp. that induces (1) reduced mortality of prey and predatory fish in forests, due to high shelter and food availability, respectively, and (2) net immigration of fish into forests due to their preference for this structurally complex habitat. Moreover, *Cystoseira* spp. may be an important source of organic matter to the ecosystem. This possible trophic role deserves complementary studies.

This work suggests that *Cystoseira* forest degradation are harmful to fish and from this perspective stresses the need to better manage human activities impacting *Cystoseira* spp..

Keywords:

Marine ecology; habitat shift; habitat structural complexity; prey-predator relationships; differential mortality; habitat selection; source of organic matter; shelter role; trophic role

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Chapitre 1 (version française). Introduction générale

1 Les écosystèmes marins côtiers menacés

A l’échelle mondiale, durant les dernières décennies, une importante proportion de la population humaine s’est accumulée dans les zones côtières, accompagnée des activités industrielles productives et extractives inhérentes au développement de ces sociétés. De plus, les récentes prédictions suggèrent une augmentation de la population humaine en zones côtières encore plus soutenue d’ici 2030 (Duedall & Maul 2005). Cette tendance s’explique par les nombreux biens et services que fournissent ces écosystèmes à l’Homme (Martínez *et al.* 2007). Les zones marines côtières sont généralement constituées d’habitats peu profonds, complexes et hétérogènes (Encadré 1), qui reçoivent d’importantes entrées de matières organiques provenant (1) du continent *via* les eaux de surfaces et les eaux souterraines, et (2) de strates d’eaux marines plus profondes *via* les phénomènes d’upwelling (Gattuso *et al.* 1998). Grâce à ces spécificités d’habitats, les écosystèmes marins côtiers hébergent des communautés très diversifiées et comptent parmi les écosystèmes les plus productifs de la planète (Martínez *et al.* 2007). Toutefois, la biodiversité et les fonctions des écosystèmes côtiers sont exposées à de nombreux impacts anthropiques ; l’exploitation directe des ressources marines et d’autres activités non extractives menacent potentiellement leur intégrité (Halpern *et al.* 2008).

La dégradation des habitats est reconnue comme une menace majeure pesant sur les écosystèmes terrestres, aquatiques et marins (Chapin *et al.* 2000; Keith *et al.* 2013). Elle peut affecter les processus écologiques déterminant l'abondance et la distribution des organismes, altérer la structure des communautés, le fonctionnement des écosystèmes et leur capacité de résistance et résilience. *In fine*, cela peut réduire le potentiel des écosystèmes à fournir durablement des biens et services à l'Homme (Chapin *et al.* 2000; Folke *et al.* 2004; Cardinale *et al.* 2012). Les facteurs de perturbations d'origine anthropique qui altèrent les habitats marins côtiers sont nombreux. Ils incluent notamment la pêche (destructive ou non), la construction de corridors écologiques facilitant les invasions d'espèces (*e.g.* le Canal de Suez), la dégradation de la qualité des masses d'eaux et l'augmentation des taux de sédimentation (*e.g.* due à l'urbanisation, l'industrialisation, l'agriculture intensive, l'aquaculture), ainsi que les aménagements côtiers (*e.g.* ouvrages portuaires) (Claudet & Fraschetti 2010).

Encadré 1. Définitions

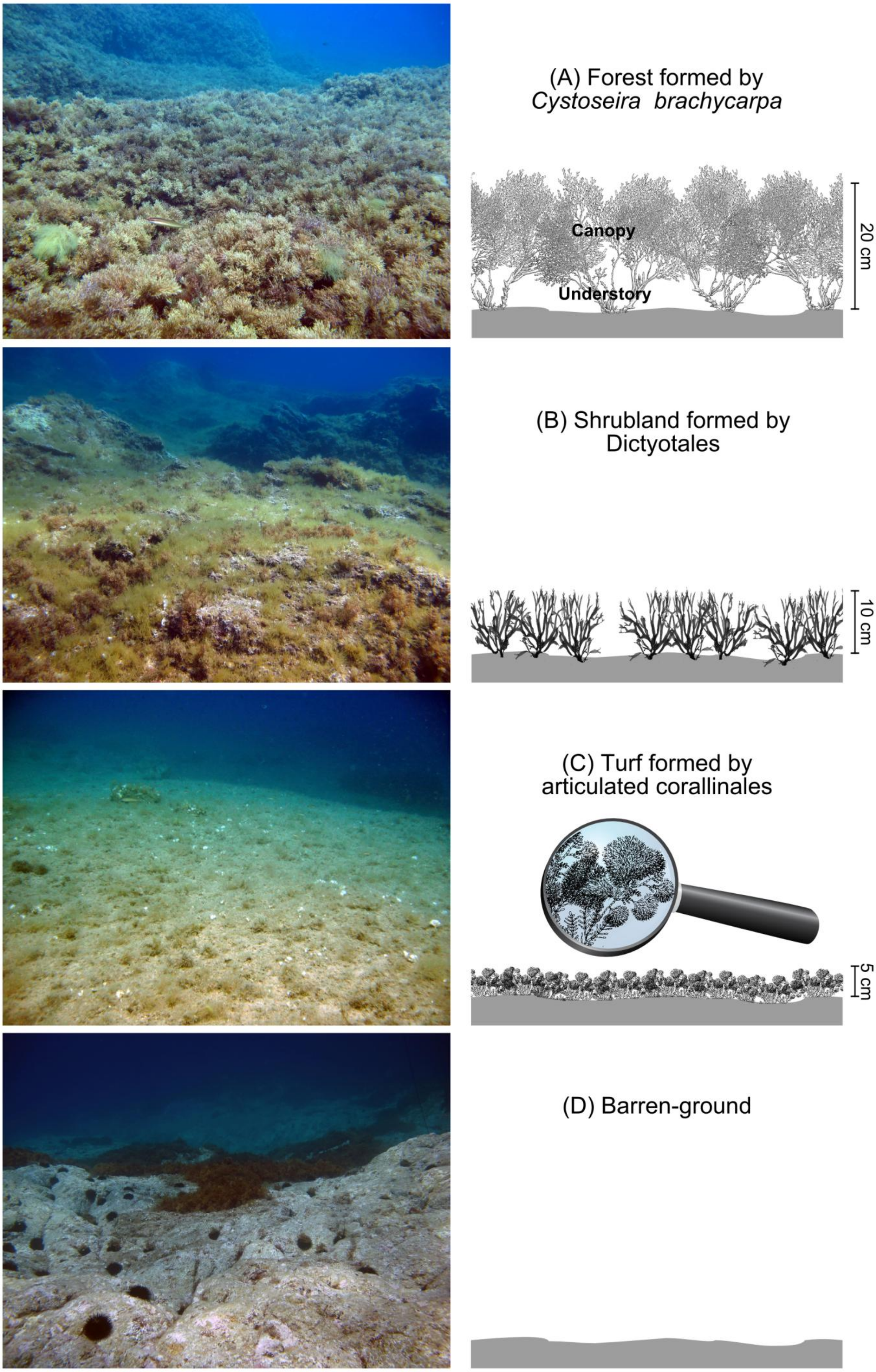
Le terme "**Habitat**" ne fera pas référence dans ce manuscrit à la notion "espèce-centrée" d'habitat, mais fera plutôt référence au concept de "**Biotope**", *i.e.* d’unité organisationnelle fondamentale des écosystèmes (Olenin & Ducrotoy 2006). Le terme "Habitat" évoquera donc une sous-partie du paysage sous-marin (> 100 m²), défini selon des caractéristiques physico-chimiques et biologiques (principalement la topographie, le type de substrat et le type de végétation), auxquelles sont généralement associés une biocénose particulière et un certain fonctionnement écosystémique local (Törnroos *et al.* 2013). Par exemple, cette définition désigne comme habitat l'herbier à *Posidonia oceanica*.

La **complexité structurelle d'un habitat** découle de la quantité et de la composition des éléments solides (abiotiques et biotiques) présents au sein de cet habitat (McCoy & Bell 1991; Beck 2000; Byrne 2007). Les éléments abiotiques structurant "l'architecture" d'un habitat dépendent principalement de la géomorphologie du substrat et incluent par exemples les rochers, crevasses, cavités, surplombs, *etc*. (e.g. Gimenez-Casalduero *et al.* 2011). Les éléments biotiques comprennent principalement les macrophytes (algues, plantes) et les invertébrés sessiles (*e.g.* coraux, huitres) (Thomsen *et al.* 2010).

2 La dégradation des habitats dans l'Infralittoral rocheux Méditerranéen

Dans l'Infralittoral rocheux Méditerranéen, les espèces du genre *Cystoseira* (Fucales) sont de grandes algues brunes pouvant former une canopée et constituer ainsi des habitats semblables à des forêts, appelées "forêts à *Cystoseira*" (Clarisse 1984) (Figure 1A). La plupart des espèces du genre *Cystoseira* sont sensibles aux perturbations d'origine anthropique et leur population ont régressé (et régressent encore) dans toute la Mer Méditerranée (Thibaut *et al.* 2005; Bianchi *et al.* 2012; Gianni *et al.* 2013; Bianchi *et al.* 2014). En fonction de l'identité et de l'intensité des perturbations anthropiques, les forêts à *Cystoseira* ont été (sont) remplacées par des habitats structurellement moins complexes. Dans les zones côtières où la qualité des masses d'eau a été (est) dégradée (*e.g.* augmentation de la turbidité et du taux de sédimentation, enrichissement en nutriments, pollution), les forêts à *Cystoseira* ont été (sont) généralement remplacées par des assemblages de macroalgues dominés par (1) des Dictyotales et/ou Sphacélariales qui forment des habitats semblables à des brousses (*shrublands* en anglais, Figure 1B), ou (2) des Corallinales articulées qui forment des habitats semblables à des gazons (*turfs* en anglais, Figure 1C) (Airoldi & Beck 2007; Mangialajo *et al.* 2008). Dans les zones côtières où ont été (sont) pratiquées la pêche à la datte de mer (*Lithophaga lithophaga*) et/ou de la surpêche des poissons prédateurs d'oursins (principalement les Sparidae du genre *Diplodus*), les forêts à *Cystoseira* ont été (sont) remplacées par des fonds désertiques (*barrens* en anglais, Figure 1D), où seuls des Corallinales encroûtantes et des invertébrés sessiles se développent, accompagnés généralement de grandes densités d'oursins (Guidetti *et al.* 2004; Guidetti 2006; Hereu *et al.* 2008). De meilleures mesures de gestions visant à réduire ces perturbations anthropiques (régulation des pêches, amélioration du traitement des eaux usées) pourraient permettre la restauration des forêts à *Cystoseira.* Toutefois, cela a rarement été observé. A ce jour, la restauration de populations de *Cystoseira* spp. n'a été scientifiquement prouvé que dans la Réserve Marine des îles Médès (Sala & Boudouresque 1997; Hereu *et al.* 2008). L'explication consensuelle de cette quasi-absence de restauration serait que les propagules de *Cystoseira* spp. ont une capacité de dispersion très limitée. Par conséquent, la restauration naturelle de forêts à *Cystoseira* serait cantonnée à une recolonisation pas-à-pas depuis des populations non dégradées (sources de propagules), ce qui peut être contraint par la présence de barrières géographiques (Mangialajo *et al.* 2012; Gianni *et al.* 2013; Robvieux 2013).

Figure 1 (page de droite). Quatre types d'habitats dans l'Infralittoral rocheux Méditerranéen. Les photos ont été prises en Corse pendant l'été 2011, à 8 m de profondeur. Le premier plan couvre environ 2 m de largeur. Les schémas représentent la complexité structurelle de l'habitat formé par les macroalgues dominantes.


(A) Forest formed by
Cystoseira brachycarpa
Canopy
Understory
20 cm
(B) Shrubland formed by
Dictyotales
10 cm
(C) Turf formed by
articulated corallinales
5 cm
(D) Barren-ground

3 Les peuplements de poissons sont-ils affectés par la régression des forêts à *Cystoseira*?

Pour évaluer les éventuelles conséquences pour les communautés fauniques de la régression des forêts à *Cystoseira*, l'approche la plus directe consisterait à comparer temporellement la structure des communautés fauniques dans les mêmes zones côtières, avant et après la régression des forêts à *Cystoseira*. Cela nécessite de contrôler les possibles variations temporelles dues à d'autres facteurs en comparant au cours du même intervalle de temps des zones contrôles dans lesquelles les forêts à *Cystoseira* n'ont pas régressé. Cela correspond à une approche nommée en anglais *Before-After-Control-Impact*. Toutefois, cette approche ne peut habituellement pas être employée à cause du manque de données historiques concernant la structure des communautés fauniques avant que les forêts à *Cystoseira* ne régressent (voir toutefois Bianchi *et al.* 2014). C'est pourquoi l'évaluation des conséquences pour les communautés fauniques de la régression des forêts à *Cystoseira* ne peut être réalisée que par l'utilisation d'une approche appelée *Space-for-time* (ou *After-Control-Impact*), qui consiste à comparer spatialement la structure des communautés fauniques entre des zones côtières où les forêts à *Cystoseira* ont disparu et d'autres zones où les forêts à *Cystoseira* sont encore présentes. Ainsi, dans la suite de ce manuscrit, la notion de "conséquences de la régression des forêts à *Cystoseira*" sera principalement abordée en termes de différences entre zones dégradées et zones non dégradées (comparaison spatiale), plutôt qu'en termes de différences entre avant et après la dégradation (comparaison temporelle).

Les éventuelles conséquences de la régression des forêts à *Cystoseira* pour les peuplements de poissons côtiers méritent d'être étudiées en profondeur, puisque les poissons côtiers sont particulièrement importants socio-économiquement et écologiquement. D'un point de vue socio-économique, ils sont notamment exploités par la pêche professionnelle artisanale (dit *au petit métier*), *e.g.* plus de 1500 bateaux commerciaux artisanaux étaient immatriculés en Méditerranée française en 2011 (Etude du Conseil Consultatif Régional de la Mer 2013). De plus, les poissons côtiers sont visés par les pêcheurs récréatifs, *e.g.* il a été estimé environ 2,5 millions de pêcheurs récréatifs en France métropolitaine en 2005 (Herfaut *et al.* 2013). D'un point de vue écologique, les poissons côtiers sont importants, notamment car ils assurent diverses fonctions trophiques (d'herbivores à grands prédateurs) et sont donc essentiels au fonctionnement global des écosystèmes côtiers (Holmlund & Hammer 1999). Malgré l'importance des poissons côtiers et le fait qu'ils figurent parmi les compartiments les plus étudiés, il existe un manque général de données historiques quant à la structure (composition et densités) des peuplements de poissons avant que les forêts à *Cystoseira* ne régressent.

A ce jour, très peu d'études ont évalué les possibles conséquences de la régression des forêts à *Cystoseira* pour les peuplements de poissons. Certains sous-ensembles du peuplement de poissons (des sélections d'espèces et/ou de stades de vie) ont été comparés entre des zones présentant des forêts à *Cystoseira* et des zones présentant d'autres habitats rocheux structurellement moins complexes. Ils incluent principalement les poissons necto-benthiques aux stades juvéniles (Cheminée 2012; Cheminée *et al.* 2013) et adultes (Orlando Bonaca & Lipej 2005; Giakoumi *et al.* 2012; Sala *et al.* 2012; Giakoumi & Kokkoris 2013). Certaines de ces études avaient également échantillonné les poissons crypto-benthiques, mais elles avaient utilisé pour cela des méthodes de comptages visuels qui sont reconnues pour leur sous-estimation chronique de la diversité et de la densité des poissons crypto-benthiques (Ackerman & Bellwood 2000; Willis 2001; Smith-Vaniz *et al.* 2006; Bozec *et al.* 2011).

Il apparait ainsi que les éventuelles conséquences de la régression des forêts à *Cystoseira* pour l'ensemble du peuplement de poissons, *i.e.* à la fois les poissons crypto- et necto-benthiques, restent fort méconnues. Ceci conduit à la première question soulevée par ce projet de thèse :

- ❖ Q1: La structure des peuplements de poissons (crypto- et necto-benthiques) est-elle différente entre les forêts à *Cystoseira* et les autres habitats rocheux structurellement moins complexes?

4 Quels sont les processus écologiques sous-jacents ?

Lorsque des différences dans la structure des peuplements de poissons sont détectées entre habitats dégradés et non dégradés (indiquant des potentielles conséquences de la dégradation des habitats), l'étape suivante consiste à identifier les processus écologiques responsables de ces différences. En effet, une meilleure connaissance de ces processus peut éventuellement permettre d'envisager de mettre en œuvre des méthodes de conservation et/ou restauration.

Les dégradations d'habitats telles que les changements dans la structure des peuplements de macrophytes peuvent affecter plusieurs processus écologiques qui structurent les peuplements de poissons. Les principaux processus ont été identifiés grâce à une étude bibliographique présentée dans le Chapitre 2 de ce manuscrit. Synthétiquement, les macrophytes sont des producteurs primaires qui peuvent être des sources de matière organique soutenant le réseau trophique. Les macrophytes sont également des organismes "formeurs d'habitat". Ils peuvent influencer la complexité structurelle de l'habitat, en fonction de leurs caractéristiques morphologiques et de leur densité. Ainsi, un changement dans la structure des peuplements de macrophytes peut potentiellement changer la nature et la quantité de nourriture et d'abris disponibles pour les poissons. Ces potentiels changements dans la disponibilité en nourriture et abris (éventuellement des refuges face aux prédateurs) peuvent influencer la mortalité des poissons induite par famine et par prédation, de même que leur comportement lorsqu'ils sélectionnent leur espace de vie (*i.e.* préférence pour un habitat). *In fine*, des différences de mortalité entre habitats et/ou la préférence de certains poissons pour un habitat en particulier, peuvent tous deux générer des différences entre habitats dans la composition et les densités des peuplements de poissons.

Le présent projet de thèse a visé à mieux comprendre comment les macroalgues, en fournissant de la complexité structurelle à l'habitat, peuvent affecter la composition et les densités des peuplements de poissons. Une attention particulière a été portée aux potentiels effets des macroalgues sur les interactions létales et comportementales entre poissons proies et prédateurs ainsi que sur leurs préférences d'habitats, en s'intéressant aux questions suivantes:

- ❖ Q2 : Est-ce que la plus grande complexité structurelle des forêts à *Cystoseira* augmente la survie des poissons proies / réduit l'efficacité des poissons prédateurs?

- ❖ Q3 : Comment la complexité structurelle de l'habitat influence le comportement anti-prédateur des poissons proies (*e.g.* tactique de fuites) et la stratégie alimentaire des prédateurs?

- ❖ Q4 : Est-ce que la complexité structurelle de l'habitat influence les décisions prises par les proies et les prédateurs, lorsqu'ils choisissent leur espace de vie (*i.e.* préfèrent-ils un habitat) ?

- ❖ Q5 : Est-ce que les décisions prises par les poissons proies lorsqu'ils choisissent leur espace de vie, sont influencées par la présence de prédateur, et *vice versa* ?

Le présent projet de thèse a également visé à décrire plus globalement le réseau trophique des forêts à *Cystoseira* en soulevant notamment la question suivante :

- ❖ Q6: Est-ce que les *Cystoseira* spp., en tant que producteurs primaires, représentent d'importantes sources de matière organique pour le réseau trophique ?

5 Approches employées et structure du manuscrit

Pour aborder ces questions, plusieurs approches complémentaires ont été employées : synthèses bibliographiques, inventaires de macroalgues et de poissons, expériences en aquariums, analyses de compositions isotopiques et de contenus stomacaux. Dans cette perspective, le présent manuscrit est écrit sous forme de chapitres/articles interconnectés, dont les approches et objectifs respectifs furent :

Chapitre 2 : Une synthèse de la bibliographie - Présenter les principaux processus écologiques qui déterminent les patrons de distributions (spatiales) des poissons et montrer comment les macroalgues peuvent affecter certains de ces processus.

Chapitre 3 : Des inventaires de terrain - Comparer la structure de l'ensemble du peuplement de poissons entre les forêts à *Cystoseira brachycarpa* et les habitats structurellement moins complexes de types *turf* et *barren* (Question 1).

Chapitre 4 : Des expériences en aquariums - Déterminer comment la complexité structurelle formée par les macroalgues peut affecter les interactions proies-prédateurs et les décisions prises par les poissons lorsqu'ils choisissent leur espace de vie (Questions 2 à 5).

Chapitre 5 : Des analyses de compositions isotopiques et de contenus stomacaux - Estimer le régime alimentaire des poissons macrocarnivores vivant dans les forêts à *Cystoseira brachycarpa*, afin de déterminer si effectivement ils réussissent à chasser d'autres poissons malgré la grande complexité structurelle (Question 2), et décrire la structure trophique de l'écosystème forêt à *C. brachycarpa* (Question 6).

Chapitre 6 : Une discussion générale - Synthétiser et discuter tous les résultats obtenus et envisager des perspectives.

Les chapitres 2 à 5 reprennent des manuscrits rédigés en langue anglaise déjà soumis ou prochainement soumis, ils sont donc intégrés comme tels dans le présent manuscrit. Le présent chapitre 1 (Introduction générale) ainsi que le chapitre 6 (discussion générale) sont présentés en langues française et anglaise.

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Chapter 1 (english version). General Introduction

1 Marine coastal ecosystems under threats

On a global scale it has been widely reported that significant proportions of human populations have accumulated on coastal zones in the last decades, along with related coastal urbanization, and productive and extractive activities. Recent projections, in addition, suggest the possibility of a further dramatic increase in coastal populations for the next quarter of 21th century (Duedall & Maul 2005). The main reason for explaining this trend is that coastal systems provide important ecosystem goods and services that produce benefits to humans (Martínez *et al.* 2007). Coastal waters usually host heterogeneous and complex shallow habitats (Box 1) and receive considerable inputs of nutrients and organic matter coming from the continent through surface runoff or groundwater flow, or from deeper stands through upwelling (Gattuso *et al.* 1998). Heterogeneity and productivity are among the main reasons that could explain why coastal marine ecosystems usually host highly diversified marine communities, and are among the most productive systems of the planet (Martínez *et al.* 2007). However, biodiversity and ecosystem functions related to coastal ecosystems are severely exposed to a wide array of human impacts, such as direct exploitation and other non-extractive activities, potentially threatening their integrity (Halpern *et al.* 2008).

Habitat degradation is recognized as a major threat to terrestrial, aquatic and marine ecosystems (Chapin *et al.* 2000; Keith *et al.* 2013). This may affect ecological processes underlying abundances and distributions of organisms, community structures, the whole functioning of ecosystems, and their resistance and resilience. Ultimately, this may reduce ecosystems' potential to provide sustainably good and services to humans (Chapin *et al.* 2000; Folke *et al.* 2004; Cardinale *et al.* 2012). Anthropogenic stressors that impact coastal habitats include fisheries (destructive or not), building of corridors facilitating species invasion (*e.g.* Suez Canal), sedimentation increase and water quality degradation (*e.g.* due to urbanization, industrialization, intensive agriculture, aquaculture), and land claims (Claudet & Fraschetti 2010).

Box 1. Definitions

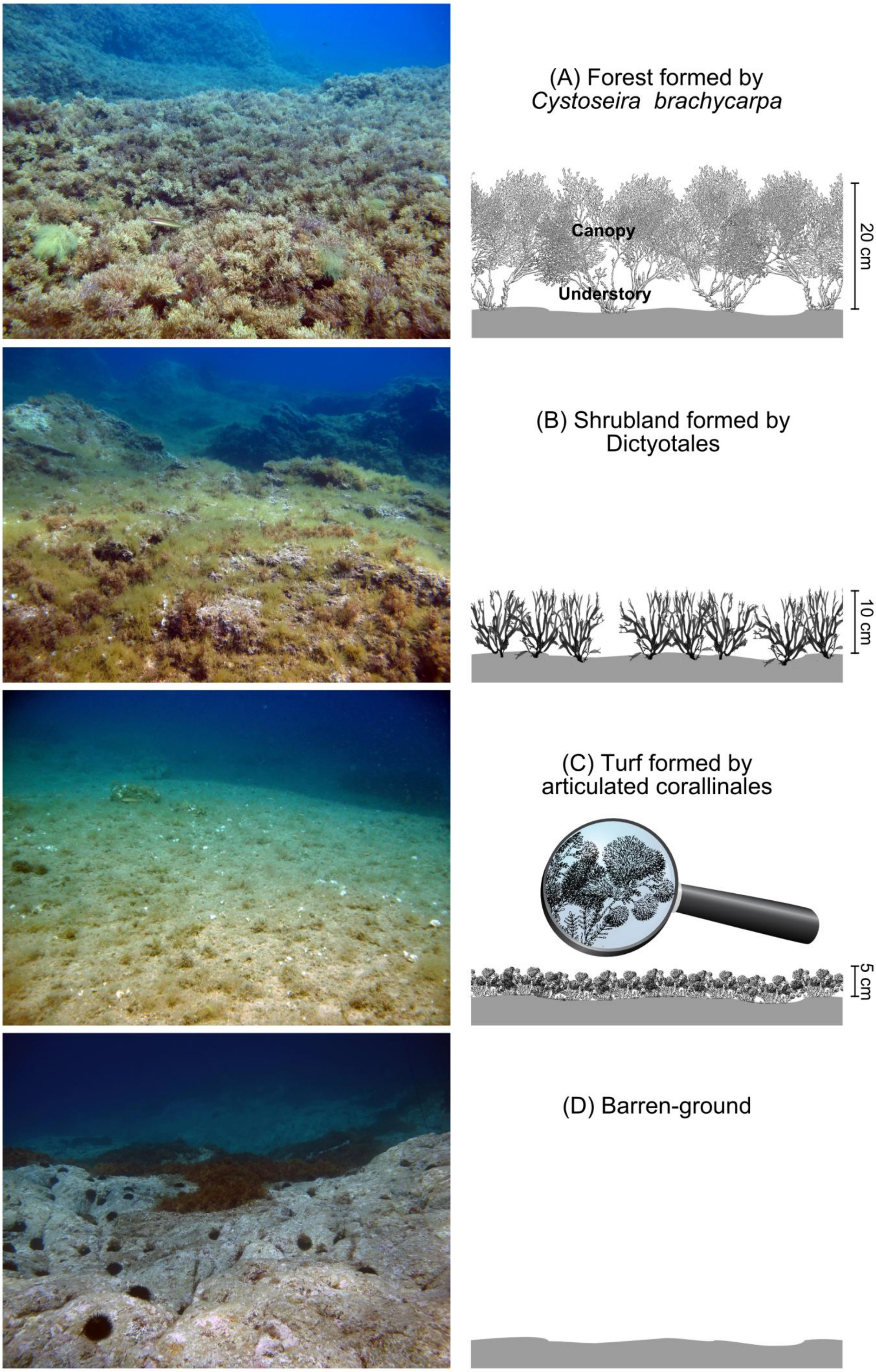
Habitat will not refer in this manuscript to the species-specific notion of habitat, but rather to the concept of **Biotope,** *i.e.* a fundamental organizational unit of coastal ecosystems (Olenin & Ducrotoy 2006). Habitat will therefore refer to a sub-unit of the seascape (> 10^2 m^2), recognizable based on physical-biological structures (mainly topography, type of primary substrate, and vegetation types), as surrogates for the whole biocenosis and local ecological functioning (Törnroos *et al.* 2013). For instance, this definition includes as habitat *Posidonia oceanica* meadows.

Habitat structural complexity equates the amount and composition of physical elements (both abiotic and biotic) within an habitat (McCoy & Bell 1991; Beck 2000; Byrne 2007). Abiotic elements shaping a habitat include mainly geo-morphological features (*e.g.* presence of boulders, crevasses, caves, overhangs)(*e.g.* Gimenez-Casalduero *et al.* 2011). Biotic elements include mainly macrophytes (seagrasses, mangrove roots, kelps) and sessile invertebrates (*e.g.* corals, oysters) (Thomsen *et al.* 2010).

2 Habitat degradation in subtidal Mediterranean rocky reefs

In subtidal Mediterranean rocky reefs, *Cystoseira* species (Fucales), large canopy-forming brown algae, may form forest-like habitats called '*Cystoseira* forests' (Clarisse 1984)(Figure 1A). Most of *Cystoseira* species are sensitive to direct and indirect human impacts, and their regression has been recorded across the entire Mediterranean (Thibaut *et al.* 2005; Bianchi *et al.* 2012; Gianni *et al*. 2013; Bianchi *et al.* 2014) and is still ongoing. Depending on the identity and intensity of anthropogenic stressors, *Cystoseira* forests can (have) be(en) replaced by less structurally complex habitats. In areas with degraded water quality (*e.g.* increase in turbidity and sedimentation rate, nutrient enrichment, or pollutant), *Cystoseira* forests disappear(ed) and usually macroalgal assemblage (did) become dominated by Dictyotales and/or Sphacelariales, that form shrublands-like habitats (Figure 1B), or dominated by articulated Corallinales that form turf-like habitats (Figure 1C) (Airoldi & Beck 2007; Mangialajo *et al.* 2008). In areas where date-mussel fishery and/or overfishing (especially of the sea breams) occur(ed), *Cystoseira* forest are (were) replaced by barren grounds, *i.e.* bare rocks with only encrusting coralline algae and sessile invertebrates, and usually high densities of sea urchins (hereafter called 'barren', Figure 1D)(Guidetti *et al.* 2004; Guidetti 2006; Hereu *et al.* 2008). Better management practices for reducing anthropogenic stressors (*e.g.* fishing regulation, waste water treatments) might allow recovery of formerly abundant *Cystoseira* forests. However, it has rarely been observed (only *Cystoseira* spp. recovery in Medes Islands Marine Reserve has been documented: Sala & Boudouresque 1997; Hereu *et al.* 2008). The consensual explanation for the absence of *Cystoseira* spp. recovery is that sexual propagules of *Cystoseira* spp. have really low dispersion abilities, and consequently natural recovery of *Cystoseira* forest is limited to step-by-step recolonization from populations that persisted, which may be constrained by geographical barriers (Mangialajo *et al.* 2012; Gianni *et al.* 2013; Robvieux 2013).

Figure 1 (right-hand page). Four habitat-types in North-Western Mediterranean subtidal rocky reefs. Left panel: pictures taken in Corsica during summer 2011, at 8 m deep. Foregrounds span around 2 m width. Right panel: schematic representations of the habitat structure provided by the dominant macroalgae.


(A) Forest formed by
Cystoseira brachycarpa
Canopy
Understory
20 cm
(B) Shrubland formed by
Dictyotales
10 cm
(C) Turf formed by
articulated corallinales
5 cm
(D) Barren-ground

3 Do habitat degradations affect fish assemblages?

For assessing the consequences of *Cystoseira* forests collapses on faunal communities, the straightforward approach would consist in comparing faunal communities structures in the same areas between before and after *Cystoseira* forests collapsed, while controlling possible temporal variations due to other factors through the temporal comparison of some control areas where *Cystoseira* forests did not collapse: *i.e.* a 'Before-After-Control-Impact' approach. However, this approach is usually not possible due to a general lack of historical data on faunal communities structures before *Cystoseira* forests collapsed (although, see Bianchi *et al.* 2014). Consequently, the assessment of putative effects of habitat degradations on faunal communities, can be achieved only through the use of a 'space-for-time' approach, by comparing faunal communities between areas where *Cystoseira* forests are still present and other areas where *Cystoseira* forests had been replaced by other macroalgae assemblages. Hence, hereafter the notion of 'habitat degradation consequences' will be mainly addressed in terms of differences between degraded and non-degraded habitats (spatial comparisons), rather than in terms of differences between before and after habitat degradation occurred (temporal variations).

Putative effects of coastal habitat degradation on fish assemblage structure (composition and densities) deserve to be studied in depth since coastal fishes are particularly important both socio-economically and ecologically. Socio-economically, because coastal fishes are exploited by commercial small-scale artisanal fisheries, *e.g.* more than 1500 commercial artisanal fishing boats were licensed in French Mediterranean in 2011 (Etude du Conseil Consultatif Régional de la Mer 2013). Moreover, coastal fishes are targeted by recreational fishermen, *e.g.* estimations suggested around 2.45 million recreational (mainly coastal) fishermen in metropolitan France in 2005 (Herfaut *et al.* 2013). Ecologically, because coastal fishes cover diverse trophic functions from herbivorous to high-level predators, and are therefore essential for sustaining the whole ecosystem functioning (Holmlund & Hammer 1999). Despite fishes are important and among the most studied compartments, there is also a lack of historical data on fish assemblage structure before *Cystoseira* forests collapsed, and really few studies assessed the putative consequences of habitat degradation on fish.

Some subsets of the whole fish assemblage had been compared between *Cystoseira* forest and other macroalgae assemblages. It included mainly necto-benthic fish juveniles (Cheminée 2012; Cheminée *et al.* 2013) and necto-benthic fish adults (Orlando Bonaca & Lipej 2005; Giakoumi *et al.* 2012; Sala *et al.* 2012; Giakoumi & Kokkoris 2013). These latter studies also sampled crypto-benthic fish, but through the use of underwater visual census that is a method well known for underestimating crypto-benthic fish diversity and abundances (Ackerman & Bellwood 2000; Willis 2001; Smith-Vaniz *et al.* 2006; Bozec *et al.* 2011).

It appeared therefore that the consequences of *Cystoseira* forests collapse on the whole fish assemblage, *i.e.* both crypto- and necto-benthic fish, were poorly known. This raised the first main question that addresses the present PhD project:

- ❖ Q1: Are crypto- and necto-benthic fish assemblage structures different between *Cystoseira* forests and the other macroalgae assemblages?

4 What are the ecological processes underlying the effects of habitat degradation on fish distribution patterns?

Once an impact on distribution patterns have been detected, the step forward consists in investigating through which ecological process the impact occurred. This may allow to consider the possibility to develop conservation and/or restoration actions.

Shifts in macroalgae assemblage structure may affect several ecological processes that underlie fish distribution patterns. They have been synthesized from the literature in the second chapter of this manuscript. Synthetically, macroalgae are primary producers that may act as source of organic material into the food web. Macroalgae are also habitat former, which affect structural-complexity of habitat as a function of macroalgae morphological features and densities. Therefore, shift in macroalgal assemblage structure might potentially change availabilities of food resources and shelter (eventually against predation). Putative changes in food and shelter availability may potentially affect starvation- and predation- induced mortality of fish as well their decision making in regard to habitat selection. Ultimately, differential mortality between habitats and/or habitat selection may affect fish distribution patterns among habitats.

The present PhD work investigated how habitat structural complexity provided by macroalgae may affect fish distribution patterns, by mediating behavioral and lethal interactions between prey fish and predatory fish. The following questions were addressed:

- Q2: Does the higher structural complexity of *Cystoseira* forest, increase the prey survival / reduce the predator foraging efficiency?

- Q3: How habitat structural complexity affects anti-predator behavior of prey fish (*e.g.* escape tactic) and foraging strategy of predatory fish, in terms of micro-habitats use and activity levels?

- Q4: Does habitat structural complexity affect prey and predatory fish decision making in regard to habitat selection?

- Q5: Is the prey's habitat selection affected by the presence of predator, and inversely?

The present PhD work also investigated more broadly the trophic structure of *Cystoseira* forest and addressed notably the question:

- Q6: Are *Cystoseira* spp., as primary producer, important sources of organic material to the food web?

5 Approaches used and structure of the manuscript

To address these questions, multiple complementary approaches were developed: literature synthesis, macroalgae and fish inventories, tank experiments, and stable isotopes and stomach content analyses. In this perspective, the manuscript is written as interconnected chapters/papers, whose specific approaches and goals were:

Chapter 2 - a literature synthesis: to introduce the main ecological processes that underlie fish distribution patterns among habitats and how macroalgae may affect some of these processes.

Chapter 3 - field inventories: to compare the whole fish assemblage structure between *Cystoseira brachycarpa* forests, and the less structurally complex habitat-types Turf and Barren (Question 1).

Chapter 4 - tank experiments: to investigate how habitat-complexity formed by macroalgae may affect fish prey-predator interactions, in terms of predation mortality, prey and predator habitat choices, and anti-predator behavior / predator foraging tactic (Questions 2 to 5).

Chapter 5 - stable isotope and stomach contents analyzes: to estimate feeding habits of macrocarnivorous fish specifically in '*C. brachycarpa* forest' for assessing if they actually prey on small-sized fish (Question 2), and to describe the trophic structure of the ecosystem '*C. brachycarpa* forest' (Question 6).

Chapter 6 - a general discussion to synthesize and discuss all the results obtained, and to draw some perspectives.

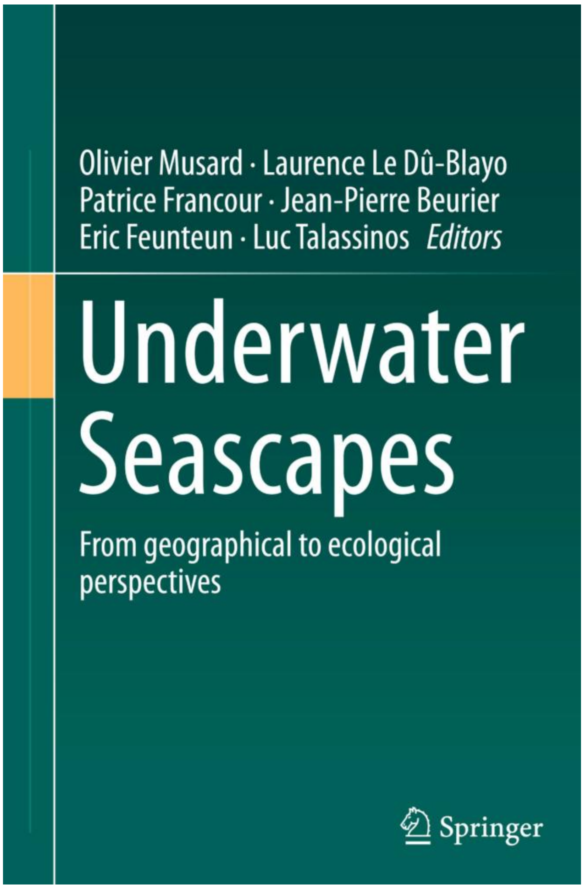
6 References

See references in the french version of this chapter, on pages 19 to 22

Chapter 2. The ecological processes structuring fish assemblages and the effects of habitat-forming macroalgae: A literature synthesis

To introduce the working hypotheses that had been tested during the present PhD work, this chapter consists of a literature synthesis on the main ecological processes that underlie fish distribution patterns among habitats. The present chapter is composed mainly by the copy of a book chapter (Thiriet *et al.* 2014) written during the first year of my PhD, and by some complements written since.

1 Copy of the book chapter 'How 3D Complexity of Macrophyte-Formed Habitats Affect the Processes Structuring Fish Assemblages Within Coastal Temperate Seascapes?'



Full references of the book chapter:
Thiriet P., Cheminée A., Mangialajo L., Francour P. (2014) How 3D Complexity of Macrophyte-Formed Habitats Affect the Processes Structuring Fish Assemblages Within Coastal Temperate Seascapes? In: O. Musard, L. Le Dû-Blayo, P. Francour, J.-P. Beurier, E. Feunteun & L. Talassinos (Eds). *Underwater Seascapes*. Springer International Publishing: 185-199.

Chapter 12
How 3D Complexity of Macrophyte-Formed Habitats Affect the Processes Structuring Fish Assemblages Within Coastal Temperate Seascapes?

Pierre Thiriet, Adrien Cheminée, Luisa Mangialajo and Patrice Francour

Abstract Macrophyte-formed habitats are important components of coastal temperate seascapes. They usually host higher diversity and density of fishes, including both adult and juvenile individuals. Here we synthesized the ecological processes underlying differences in fish assemblage structure among habitats, with an emphasis on the effects of habitat architectural complexity, which results in great part from the state of macrophyte assembalges. At a wide spatial scale, oceanographic patterns affect larval survival and dispersal and consecutive broad patterns of juvenile settlement. At a finer spatial scale, architectural complexities of the habitats affect their quality (basically food availability and predation risk) which drives local patterns of juvenile abundances through differential mortality and active habitat selection. Hence, the analysis and understanding of juvenile/adult abundance patterns have to consider nested sets of seascape features.

Keywords Fish settlement · Food availability · Shelter availability · Predation mortality · Habitat choice

12.1 What Is a Seascape from an Ecological Perspective

A seascape is a wholly or partially submerged landscape. By analogy with terrestrial landscape ecology, a seascape is a heterogeneous area that may be seen as a mosaic of patches, which belong to different types ("Patch mosaic model") (Bostrom et al.

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2011). A seascape has therefore two main features, its composition in term of patch types (e.g. combined total percent cover per patch type) and its spatial configuration, i.e. the spatial arrangement of all the patches, which may be synthesized using metrics such as number, sizes and perimeters of patches, inter-patch distances, contiguity (Wedding et al. 2011).

Patch typology intends to break down the seascape into ecologically meaningful and workable sub-units for facilitating ecological studies of the whole. Hence, each patch-type refers to a given set of environmental conditions, such as depth, type of primary substrate, availability of resources (e.g. food and shelter), and so gives insight on local ecological functioning. Therefore, patch types may be seen as benthic habitats (Fraschetti et al. 2008), the term they are usually referred as.

Ecological functioning of the whole mosaic does not simply rely on the sum of every habitat-specific ecological functioning. Patches interact together and some specific proprieties may emerge by synergy (e.g. edge effect), depending on seascape configuration (e.g. amount of ecotones) (Macreadie et al. 2010; Bostrom et al. 2011). Other environmental factors affect ecological processes (e.g. water temperature, salinity and oxygenation affect growth) and they may vary at a spatial scale distinct from patch scale, usually at broader spatial scales (Ordines et al. 2011). Hence, multiple spatial scales have to be considered for a better understanding of the ecological processes that drive organisms' distribution patterns within a seascape.

12.2 From Macrophyte Assemblages to Seascape Configuration

Some benthic organisms greatly modify local 3D-architectural complexity. They provide habitat to many other organisms and ultimately structure the whole benthic community through "habitat cascade" (Thomsen et al. 2010). Such species are called biogenic habitat formers and include for instance corals, oysters, mangroves, seagrasses and some macroalgae (Bostrom et al. 2011). In coastal temperate seascapes, biogenic habitats include mainly seagrass meadows on soft bottom and macroalgal communities on hard bottom (Fraschetti et al. 2008). Indeed, marine macrophytes (i.e. both seagrasses and macroalgae) are tri-dimensional structures at a spatial scale from 10^{-2} to 10^{1} m (www.algaebase.org). The architectural complexity of a macrophyte-formed habitat often depends on density and complexity of tri-dimensionnal structure of a dominant species/taxonomical group. Macrophyte-formed habitats with high architectural complexity include, for instances in the Mediterranean Sea: 1/the *Posidonia oceanica* meadows due to very high density of shoots (around 600 shoots m^{-2}) (Terrados and Medina-Pons 2011) that are made of ribbon-like leaves, and 2/the *Cystoseira* forests due to the very high degree of branching of *Cystoseira* species (Chemello and Milazzo

2002) that are in medium density (around 20 individuals m^{-2}) (Hoffmann et al. 1992).

It has been reported worldwide that infralittoral habitats are subject to strong modification due to anthropogenic pressures (Coll et al. 2010), such as water pollution, coastal urbanization, boat anchoring, dredging, date mussel fisheries, or invasive species (Claudet and Fraschetti 2010). Macrophytes-formed habitats have not been spared. For instances, Mediterranean *Cystoseira* dominated assemblages have been reported to regress (Thibaut et al. 2005; Mangialajo et al. 2007; Sala et al. 2011). They are generally replaced by habitats with reduced architectural complexity, such as Dictyotales-dominated assemblages (smaller ribbon-like macrophytes), algal turfs or barren-grounds (over-grazed area where dominated by encrusting corallinales). These habitat shifts induce strong modification in compositions and configurations of seascapes, and ultimately in their whole ecological functioning (Ryall and Fahrig 2006; Claudet and Fraschetti 2010).

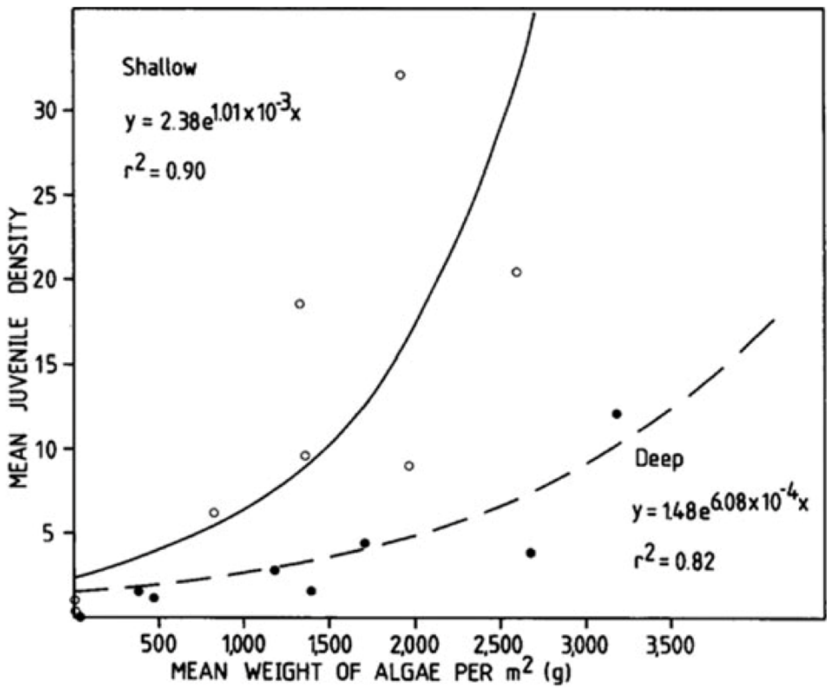
12.3 Complex Macrophyte-Formed Habitats Are Nursery for Many Fish Species

Fish assemblages usually exhibit different patterns of composition and abundances between habitats. Differences are usually larger when focusing only on post-settlement juveniles (hereafter called 'juveniles') due to their more specific habitat requirements (Harmelin-Vivien et al. 1995; Cheminée et al. 2013). The habitat(s) that host(s) higher than average densities of juveniles have a nursery role for the considered species (excluding the possible lack of connectivity with adult habitats), and are therefore very important for populations renewals (Beck et al. 2001).

Many studies carried worldwide in coastal temperate seascapes reported that macrophyte-formed habitats play the nursery role for many fish species. Examples include *Ecklonia* and *Carpophyllum* (Phaeophycea) forests of temperate rocky reefs of New Zealand (see Box 1; Jones 1984), *Cystoseira* forests of temperate rocky reefs of the Mediterranean (see Box 2; Cheminée et al. 2013) and the Mediterranean temperate *Posidonia oceanica* seagrass meadows (see Box 3; Guidetti 2000). However, it is worth noting that other less complex habitats play also the nursery role for some other species (e.g. Box 2). Hence, fish juvenile assemblage structure depends on the structure of macrophyte assemblage. We develop in the following sections how architectural complexity of macrophyte-formed habitats can affect the ecological processes structuring fish assemblages.

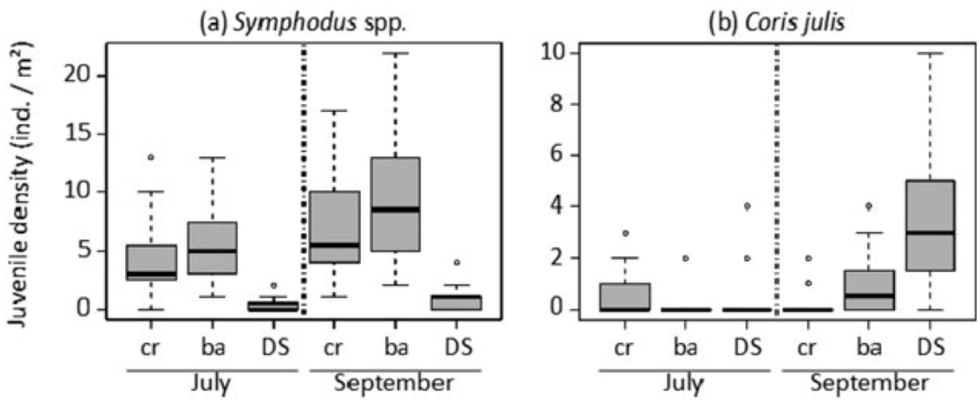
Box 1: The nursery role of a kelp forest in New Zealand—from Jones (1984)

In New Zealand, within the habitat composed by the canopy forming Phaeophyceae *Ecklonia* and *Carpophyllum*, Jones (1984) showed that mean juvenile densities of *Pseudolabrus celidotus* (Labridae) increased exponentially with the mean weight of algae per square meter. This relation was even stronger in shallow (< 8 m) than in deep (> 8 m) areas (see graph). Besides, in the same study, a macro-algal removal experiment resulted in a significantly lower juvenile fish recruitment (6 folds less juveniles per unit area in the cleared area *vs* in the control area). It was confirmed by an increased recruitment observed after the recovery of an algal forest over a previously barren rocky reef (6 folds more intense).



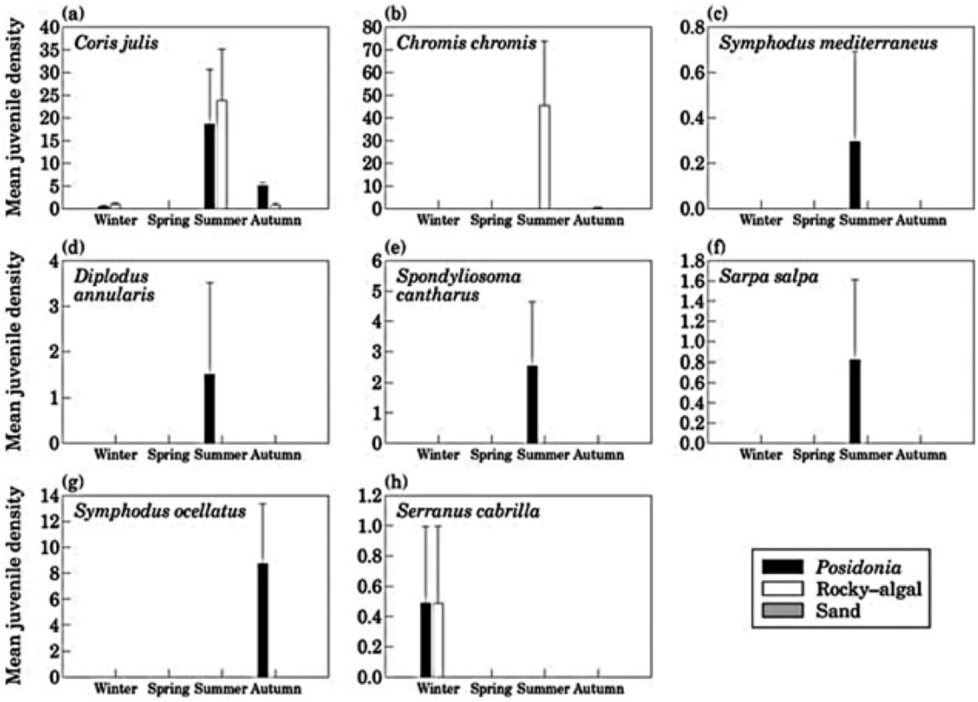
Box 2: The nursery role of Mediteranean *Cystoseira* forests—from Cheminée et al. (2013)

In 2009, Cheminée et al. (2013) compared the nursery value of distinct states of the biocenosis "photophilic macrophytes of the Mediterranean rocky infralittoral biotope". The study considered two *Cystoseira* forests (*C. crinita* [cr] and *C. balearica* [ba]) and the less complex bushy assemblage dominated by Dictyotales and Sphacelariales (DS). Juvenile fish densities of *Symphodus* spp. (box plot "a") were significantly greater in the two *Cystoseira* forests than in the bushy assemblage (DS). These differences were consistent between July (early post-settlement period) and September. They tested if abundance differences resulted from architectural complexity differences using experimental habitat manipulation. Artificially forested substratum (using *Cystoseira*-like plastic structures) had significantly greater densities of *Symphodus* spp. juveniles than the bare substratum. However contrasted response was found for other fish species in function of the considered season (box plot "b")*: Coris julis* juvenile densities were significantly higher in the bushy assemblage (DS) than in both *Cystoseira* forests, but only in autumn.



Box 3: The nursery role of Mediterranean *Posidonia oceanica* seagrass meadows—from Guidetti (2000)

Guidetti (2000) highlighted the higher nursery value for some fish species of *Posidonia* meadows in comparison to some neighboring habitats: juveniles of *Symphodus ocellatus*, *S. mediterraneus*, *Serranus cabrilla*, *Diplodus annularis*, *Spondyliosoma cantharus* and *Sarpa salpa* were significantly more abundant over *P. oceanica* meadows (black bars) than over sand habitat or rocky-algal bottom (i.e. gently sloping hard substrate covered by a dense erect assemblage of articulated Corallinaceae and *Cystoseira* spp.). Contrastingly, juveniles of *Chromis chromis* inhabited predominantly rocky-algal bottoms. Small individuals of *Coris julis* were censused over both *P. oceanica* and rocky-algal habitats. Bare sand did not host any juveniles among these species. The author suggested that differences in fish species richness and abundance are primarily related to habitat tri-dimensional structure.



Mean density (mean number of individuals of juveniles 40 m^{-2}) of common fish species. Bars indicate standard deviations

12.4 Broad Classes of Ecological Processes and Spatial Scales

Evolutionary processes have selected functional and behavioral traits that are adapted to specific environments. The selected pool of functional and behavioral traits is filtered by environments through ecological processes what governs distribution patterns of species within seascape (Morris 2011). Ecological processes may be studied according to three broad classes: (i) differential settlement/recruitment, (ii) differential mortality and (iii) active choice of the favored habitat. None of them is necessary exclusive, difference in composition and abundance of species between habitats could be the result of their combination (Olabarria et al. 2002; Morris 2003, 2011). Moreover, these processes may act at distinct spatial scales.

12.4.1 Differential Settlement Affected by Environmental Conditions at Multiple Spatial Scales

Most of demersal fish species inhabiting temperate coastal waters worldwide experience a complex life cycle. Usually, it is divided into a vagrant planktonic phase (corresponding to the stages egg and larvae) and a relatively sedentary benthic phase (from the stage post-settlers to adult) (Di Franco et al. 2011). During the planktonic phase, eggs and larvae disperse depending mainly on oceanographic patterns. The metamorphosis from larvae to juvenile triggers the transition from planktonic to benthic environment that is called "settlement". Due to oceanographic patterns (as currents, water temperature etc), juveniles that disperse may settle in greater number to one locality than to others (Di Franco et al. 2011).

In coastal environments, the seascape is usually heterogeneous at a fine spatial scale, and the different habitats are interspersed forming like a mosaic. Considering that difference in larval arrival occurs at a spatial scale that encompass habitat heterogeneity, all habitats composing one locality homogenous in term of larval arrival will exhibit the same settlement rate. According to this point, local difference in post-settlement juveniles between adjacent habitats should be due to differential mortality or movement across habitats rather than difference in larval supply. This however stresses the need to consider multiple spatial scales when studying links between habitat and post-settlement juveniles (Rilov and Schiel 2011).

12.4.2 Differential Mortality and Active Habitat Selection Affected at Finer Spatial Scales

At a finer spatial scale, assuming that the different habitats have been exposed to the same settlement rates, difference in post-settlement juveniles' densities among habitats may be due to differential mortality and/or active choice of the favored habitat. Considering that this active choice is a behavior that appeared thanks to natural selection, the chosen habitat shall be the one with the highest probability of growing and surviving until reproduction (Morris 2011). Therefore, the two classes of processes, differential mortality and active habitat selection, are both mediated by differential habitat quality in term of food availability and predation rate (Hindell et al. 2000). The highest quality habitat minimize mortality rate by offering the trade-off between foraging and safety (Anholt and Werner 1998; Dahlgren and Eggleston 2000).

12.5 Architectural Complexity of Macrophyte-Formed Habitats Interact with Processes

12.5.1 Foraging Success

Food supply is one of the basic needs for any heterotrophic organism. Food gives the energy, nutrients and vitamin needed to keep body-functioning, growth and development, and reproductive potential. Individuals experiencing starvation lose fat and muscle mass (decrease in condition) in order to keep vital systems. Growth and development of juveniles may be altered (Heck et al. 2003) as well reproductive potential of adults (Ordines et al. 2009). Energy deficiency reduces physical abilities and ultimately results in death. Low food availability may therefore causes direct mortality of post-settlement juveniles or indirect mortality through (a) a reduction of size-at-age making longer the period of vulnerability toward size-selective predation ("the bigger is better" hypothesis, Heck and Orth 1980; Levin et al. 1997), and (b) a reduction of their physical abilities to escape predator attack (Levin et al. 1997).

Availability of food resources depends on their quantity and their accessibility, which are both affected by macrophytes. Plants architecture (e.g. degree of branching) and densities affect the structure of benthic macroinvertebrate assemblages. In several regions worldwide, habitats made up structurally complex macrophytes harbor higher diversity and abundances of macroinvertebrates (Parker et al. 2001; Chemello and Milazzo 2002; Christie et al. 2009; Hansen et al. 2010). These habitats may therefore be particularly suitable as feeding grounds for invertebrate feeders such as many demersal fishes. However, it has been suggested that extremely high structural complexity may alter fishes' foraging efficiency through physical constraint (Stoner 1982; Heck and Orth 1980). Another characteristic potentially affecting invertebrate accessibility is the rigidity of macrophytes. A very flexible canopy is more sensitive to water movement and its constantly back-and-forth may limit access for fishes to understory invertebrates (Levi 2004).

12.5.2 Predation Mortality

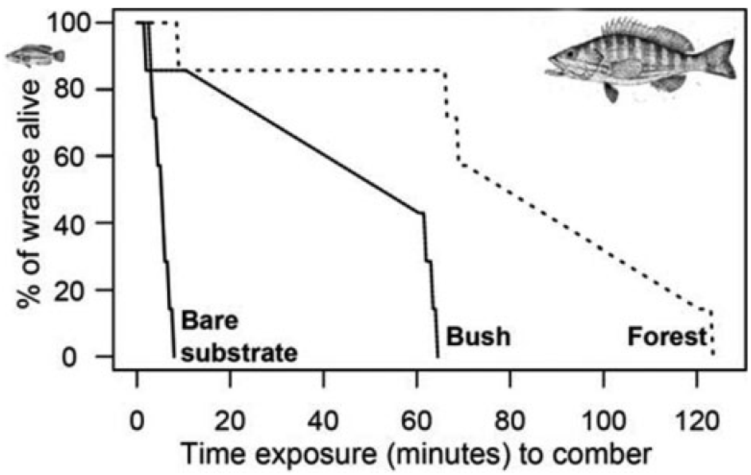
In several regions worldwide, post-settlement juveniles are known to be prey item for various predators. Predation mortality may therefore drive differences in abundance patterns of juveniles between habitats (Hindell et al. 2000; Beck et al. 2001; Heck et al. 2003). Analyzing and quantifying interactions between predators, preys and environmental factors is a quite complex task. For this purpose, the act of predation may be broken into a series of sequential stages which can be treated separately: prey detection and location by the predator, pursuit and attack, and capture (O'Brien 1979).

The predation act may be accomplished following three different broad classes of tactics. The chase (or pursuit) predator actively searches a prey item and uses its superiority in swimming speed for catching. In opposition, the sit-and-wait (or ambush) predator counts rather on the surprise. It waits motionless camouflaged in the environment until one prey enters its attack range, which is small. An intermediate tactic is used by the stalk-attack predator that actively searches for prey item. Once a prey is detected, stalk-attack predator approaches furtively until the prey is within the attack range, which is medium, and makes a speed burst to capture it (Matsuda et al. 1993; Horinouchi et al. 2009; Schultz and Kruschel 2010).

Habitat structural complexity interacts with the different stages of the predation act, what affects predation success accordingly to the tactic. In highly complex habitats, habitat-elements may interfere with prey detection/location for active searchers (chase and stalk-attack tactics), while for ambush predators, encounter rate depends only on prey density and mobility. Moreover, mobility of predators (that are most of the time larger than their prey) may be relatively more constrained by habitat-elements than prey mobility. This decreases the predation success rate sharply for chase predator (long distance pursuit) and slightly for stalk-attack predator (medium distance pursuit). As ambush tactic involves almost no predator mobility, habitat structural complexity should not facilitate prey escape. In some way, it may also be considered that habitat-elements enhance furtive wait of ambush predator and furtive approach of stalk-attack predator, for both tactics the use of camouflage has a paramount role (see Box 4) (Lima and Dill 1990; Lima 1992, 1998).

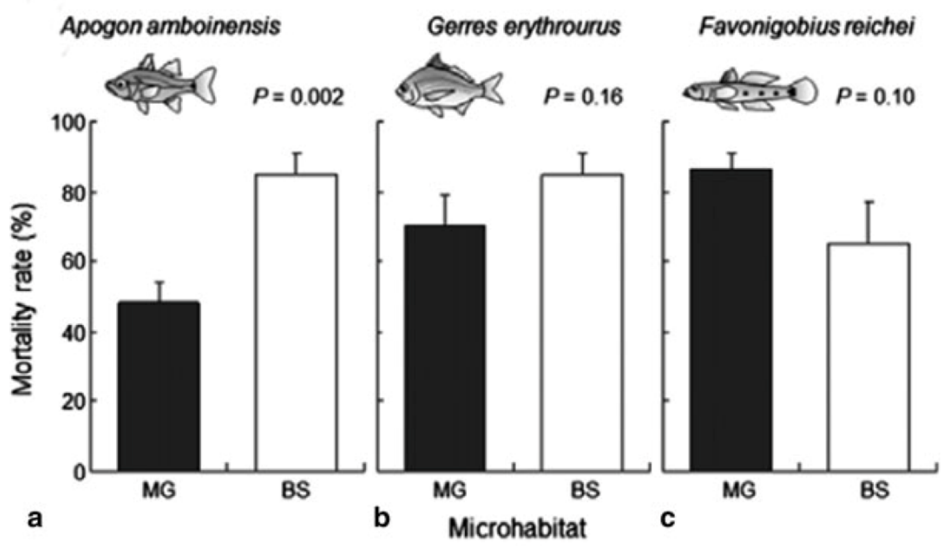
Box 4: Predation success and habitat architectural complexity—Authors' unpublished data

Thiriet et al. studied interaction between predation success and habitat architectural complexity. To avoid confounding effects with food availability, experiments were done in aquariums. Artificial habitats of increasing architectural complexity were constructed using different length of plastic algae: Bare Substrate, Bush (short stems), Forest (long stems). The biological models were two co-occurring demersal fishes in Mediterranean Infralittoral rocky reef: the comber *Serranus cabrilla* preying on post-settlement juveniles of the wrasse *Symphodus ocellatus*. Survival of one prey facing one predator was assessed in the three habitats on seven replicates. In average, survival time in Forest was 1.9- to 16.5-fold greater than respectively in Bush and Bare Substrate (see Figure). These results clearly evidence that high habitat architectural complexity may reduce predation success by providing shelter to prey. But overall predation mortality depends also on predator densities, which may be different between habitats (see Box 5).



Box 5: Predation mortality of juveniles between habitats—from Nanjo et al. (2011)
In order to compare predation mortality of juveniles between 2 different habitats (Vegetated, mangrove roots area-MG; unvegetated, bare sand area-BS), Nanjo et al. (2011) used tethering experiments, that allow to take into account both the efficiency of the predator (habitat and predation-tactic dependent, see box 4) and the density of the predator in a given habitat. The authors studied the predation rates on juveniles of three fish species: the resident, necto-benthic *Apogon amboinensis* (a), the active swimmer *Gerres erythrourus* (b) and the crypto-benthic *Favonigobius reichei* (c). For *A. imberbis*, the predation mortality was significantly lower in the vegetated habitat than in the unvegetated one, although predatory fish were more abundant in the vegetated habitat. No differences in mortality rates were found for the two other species.

These results may be explained by contrasting anti-predator tactics, either associated with mangrove structural complexity offering shelter (in the case of *A. amboinensis*) or independent of mangrove vegetation structure (for the two other species).



From these considerations, chase tactic does not seem to be suitable in highly complex habitats, while ambush tactic does. It is less clear-cut for stalk-attack tactic. Some predators are able to use only one tactic (specialist) while some others are able to use several tactics (generalist) depending on the environment. The relation between habitat and predation tactic suitability is probably a strong driver of distribution patterns of specialist predators among habitats (habitat-specific predators) (Schultz et al. 2009). Dealing with this, predation mortality of juveniles in a given habitat depends on its ability to escape the habitat-specific predators, by using different strategies such as particular microhabitat use (see Box 5). Thus, in general, coevolution between habitat-specific predator and prey juveniles results in specialized escape strategies (see Abrams 1990; Lima 1992). This specialization in escape strategy would lead the prey to actively choose for, and/or to better survive in, the habitat of its coevolved predator rather than another habitats where it has less ability to escape from predators practicing other tactics (Lima 1992).

12.6 Synergy Between Habitats: The So Called 'Edge Effect'

Previous sections report that each habitat composing the seascape has its own functioning (mediated in part by its structural complexity) what results in differential abundance patterns. However, at the boundary between two habitats (i.e. ecotone), their respective functioning affect each other and particular abundance patterns may appear in this transition area (usually higher diversity and abundance than both sides added), this phenomena is called the edge effect (Ries et al. 2004). Global increase in habitat fragmentation and its propensity to increase the amount of ecotone and consequently edge effects (Smith 2011) stresses the need to better understand underlying mechanisms.

Edge effect may come from emergent physical properties. For instance, at ecotone between marcophyte-formed habitat and bare substrate, current flow and turbulence are reduced. This may cause accumulation of swarming hyper-benthic invertebrates (such as mysids) and therefore offer a great opportunity for juveniles to forage (Macreadie et al. 2010).

Edge effect may also come from the complementarities of resources level proper to each habitat. At ecotone, mobile organisms may regularly switch between habitats and therefore exploit alternatively the optimum habitat as regard to the resource expected (basically food or shelter). For instance, one habitat may be optimum for foraging activities but with a higher predation risk than another habitat. At the ecotone, juvenile therefore can forage efficiently in the risky habitat and switch when a predator is detected. Interaction between predator tactic and structural complexity may also result in positive edge effect for prey juveniles which have developed adaptative anti predator behavior (Matsuda et al. 1993). Positioned close to the ecotone between a highly complex habitat and an open habitat, juvenile may escape in the suitable habitat as regard to the tactic of the predator detected (see section above for details about habitat-specific predators) (Martin et al. 2010; Smith et al. 2011).

12.7 Conclusions

We highlighted that analysis and understanding of juvenile abundance patterns have to consider nested sets of seascape features. At a wide spatial scale, oceanographic patterns affect larval dispersal and consecutive broad patterns of juvenile settlement. At a finer spatial scale, structural complexities of the habitats affect their quality (basically food availability and predation risk) which drives local patterns of juvenile abundances through differential mortality and active habitat selection.

Complementarities and synergies occur between habitats of a seascape. Macrophyte-formed habitats were put ahead in this chapter, because they probably have nursery role for more species than any other habitats do, in coastal temperate seascapes. But the other habitats cannot be neglected even if they have nursery role for only few species. The whole mosaic must consequently be taken into account for management practices. After decades of local-scale habitat-focused management, it is now required to upgrade coastal management at a wider seascape approach.

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2 Complements to the literature synthesis presented in the book chapter

2.1 Further details about some processes mentioned in the book chapter

2.1.1 The timing of habitat selection

In the book chapter, we did not specify when habitat selection occurs relatively to the life history stages of fish individuals. Studies suggested that for some fish species that have a bipartite life cycle (pelagic and benthic), pelagic larvae may actively choose their favored benthic habitat during settlement (Lecchini *et al.* 2007; Pollux *et al.* 2007). They could select their benthic habitat by delaying their metamorphosis and concomitant settlement, for continuing their pelagic drift until they cross their favored benthic-habitat. Experiments highlighted that pre-settlers used mainly visual cues (*e.g.* habitat structural complexity) to select their habitat (Lecchini *et al.* 2007). Also, some species (but not all) have ontogenetic habitat shifts during recruitment (when juveniles join adults). Late juveniles leave their nursery habitats and immigrate into adult habitats (Beck *et al.* 2001). Therefore, habitat selection might occur primarily during settlement and/or recruitment events (Figure S1). However, juveniles/adults that did not settle/recruit in their favored habitat might try to move over there (redistribute), depending on the composition and spatial configuration of the seascape (Beck *et al.* 2001).

2.1.2 Density-dependent processes may be triggered or not

Some processes could be density-dependent, such as starvation mortality (food limitation), predation mortality (shelter limitation) and habitat selection (trade-off foraging/safety, territory). Hence, their possible contribution in shaping fish distribution among habitats might be triggered or not, depending upon the habitat-specific availability of resources and upon the initial density of individuals (Menge 2000). Here, initial density of individuals refers to (1) the settlement rate if we consider juvenile density and post-settlement processes, or (2) the recruitment rate if we consider (sub-)adult density and post-recruitment processes.

For instance, let's be two adjacent habitats, whose one has lower food resources than the other. As long as the initial density of individuals does not reach the carrying capacity of the habitat that has the lowest food resources, starvation mortality will not be triggered in both habitats. There will be therefore no difference between habitats through this process.

Concerning habitat selection, studies on density-dependent fish spillover (net exportation) from marine reserves (Abesamis & Russ 2005) highlighted that fish may relocate their home range for reducing competition and agonistic interactions with conspecific and other competing species. From this perspective, it might be possible that when the favored habitat of a given species is overcrowded (*e.g.* due to very high recruitment rate), some individuals prefer to inhabit another habitat where competition is lower (Morris 1989; Shepherd & Litvak 2004).

Menge (2000) enunciated the 'recruit-adult' hypothesis, suggesting that the recruitment rate is a good predictor of adult density when the rate is low but not when it is high. That is, the relative contribution from recruitment *vs* post-recruitment processes varies inversely with increasing settlement rate. By analogy, we could consider the 'settler-juvenile' hypothesis, suggesting that the settlement rate is a good predictor of juvenile density when low but not when high. Considering the high spatial and temporal variability of larval supply, it is possible that from locality to locality, or from year to year, these are not the same processes (settlement *vs* post-settlement) that control juvenile densities and distribution among habitats. As well, this could reverberate on the relative contribution of recruitment *vs* post-recruitment processes in shaping adult densities and distributions among habitats.

In the context of experimental ecology, this stresses the need to consider different initial conditions in terms of individual densities (as proxies of settlement or recruitment rates) when attempting to ascertain the relative contribution of each mechanism.

2.2 Some other possible effects of macroalgae on fish

2.2.1 Macroalgae may increase eggs survival

Macroalgae as physical attributes might also facilitate eggs survival of some fish species. For instance, some *Symphodus* spp. (*e.g. S. ocellatus, S. roissali* and eventually *S. tinca*) build nests using macroalgae and notably *Cystoseira brachycarpa* (Lejeune 1985; Berghe 1992). Nests ensure better survival of eggs against predation (Lejeune 1985). Some other species, like *Symphodus melanorcercus* don't build nests. They deposit in several places few amount of eggs on the substrate, below the algae cover (Lejeune 1985; Berghe 1992). This might be an anti-predation strategy and might also be related to the reduction of hydrodynamsism below the algae cover, which may prevent eggs dislodgment. From these perspectives, macroalgae, as source material for building nest or as habitat former, might increase eggs survival.

2.2.2 Macroalgae may facilitate settlement

Besides the possible habitat selection of fish individuals during settlement, another phenomenon might increase settlement rates in structurally complex habitats. Habitat structural complexity might (1) reduce current flow and turbulence and therefore increase sedimentation rate compared to bare habitats (Macreadie *et al.* 2010), and (2) act as a mesh that trap settling individuals. This might increase settlement rates and reduce dislodgment of new settlers due to hydrodynamism, compared to bare habitats where settlers are more exposed to drift away. At our knowledge, there is no study that tested this putative effects of macrophytes on fish (see discussion in Jelbart *et al.* 2006), but hydrodynamics effects of macrophytes-formed habitats are already known to affect the distribution of other organisms such as mysids (Macreadie *et al.* 2010 and references therein). Hence, despite the 'homogenous rain of larvae' hypothesis, higher early juvenile densities (settlers) in structurally complex habitat might result from both the facilitating effect of macroalgae and the active habitat selection during settlement.

2.2.3 Macroalgae may reduce competition for space

Habitat structural complexity provides visual interference and may reduce animals field of view (Rilov *et al.* 2007). The book chapter detailed how this may affect prey-predator interactions. This might also affect competition for space, especially for territorial species. For instance, *Cystoseira* spp. canopy may potentially prevent two crypto-benthic fish to see each other even if they are very close. This might reduce agonistic behavior and the related energy costs (Abesamis & Russ 2005).

3 Conclusion

Habitat structural complexity provided by macroalgae may affect fish distribution patterns through several processes, all along fish life span (Figure 1). Macroalgae affect food and shelter availability in benthic habitats. This may affect growth and maturation, and starvation- and predation- induced mortality, eventually through density-dependent processes. Moreover, food and shelter availability may contribute in fish decision making as regards habitat selection, which may occurs during settlement and recruitment that are transitional events in life history of individuals, and/or occur after these events (redistribution). Macroalgae may also increase eggs survival, facilitate settlement, and reduce competition for space.

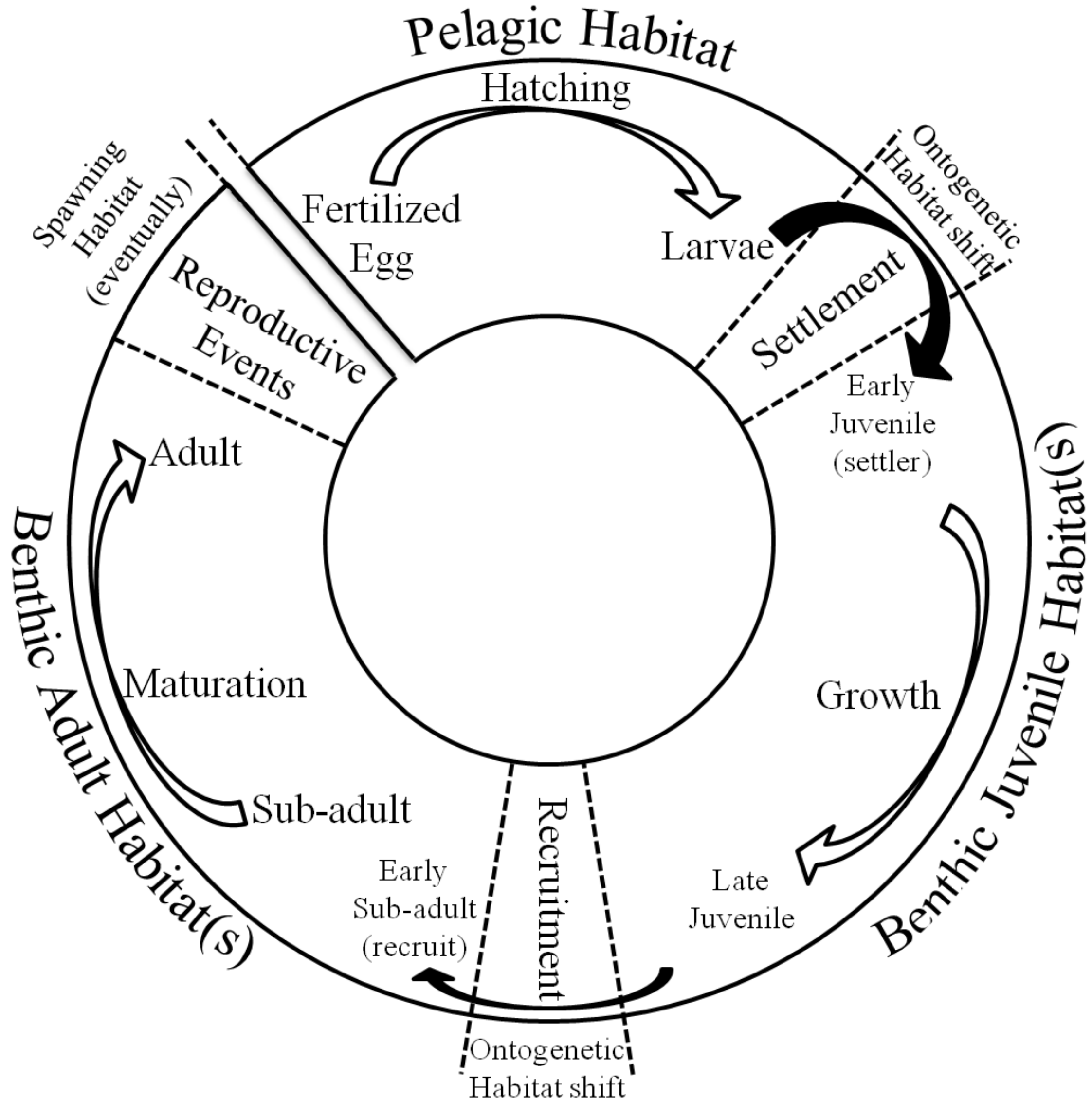

Figure 1. Life cycle of an hypothetical fish species experiencing a bipartite life cycle (pelagic *vs* benthic) and a segregation between juvenile and adult habitats.

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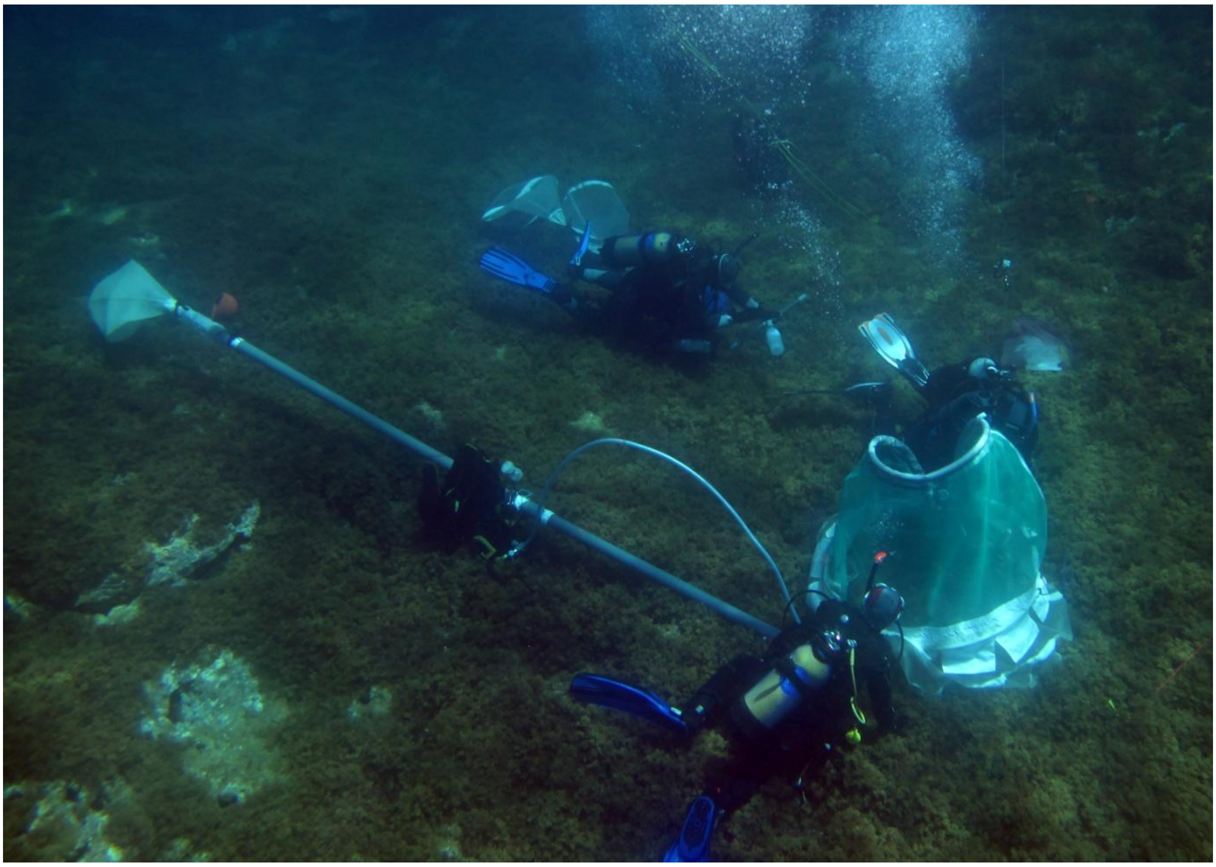
Chapter 3. Crypto- and necto- benthic fish assemblages in *Cystoseira* forests and less structurally complex habitats.



Sampling gears used for assessing crypto-benthic fish assemblage structure

This chapter will be submitted to an international journal, with the co-authors as follow:

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Abstract

In subtidal Mediterranean rocky reefs, *Cystoseira* spp. forests are regressing due to anthropogenic stressors. They are replaced by less structurally complex habitat-types such as turfs and barren grounds. We aimed to assess the consequences for coastal fish of these habitat shifts, which are poorly known. We carried a spatial comparison of fish assemblage structure between *Cystoseira brachycarpa* forests (Forest), erect articulated corallinale turfs (Turf) and barren grounds (Barren), in Corsica and Menorca. To sample the whole fish assemblage, we combined for the first time in Mediterranean the use of (1) Underwater Visual Census (UVC) for sampling necto-benthic fish, and (2) Enclosed Anesthetic Station (EAS) for sampling crypto-benthic fish, since these 'hard to spot' fish cannot be reliably sampled by UVC. Fish more abundant or present only in Forest included juveniles and adults of numerous species, small-sized crypto-benthic (Blenniidae, Gobiidae, Trypterigidae) and necto-benthic (mainly *Symphodus* spp.), and larger-sized macrocarnivores (*Serranus cabrilla*, *S. scriba, Scorpaeana porcus*). Fish more abundant in Barren were only the sea urchin feeders *Diplodus* spp., and *Thalassoma pavo* only in Mernorca. No fish was primarily associated to Turf, where densities were intermediate between Barren and Forest. As a whole, taxa richness and total density were the highest in Forest, intermediate in Turf, and the lowest in Barren. Biomass did not differ between habitat-types due to the larger body-sizes of the few fish taxa present in Barren and Turf. Irrespectively of the habitat-type, crypto-benthic fish represented in average 92 % of total fish densities and 17 % of total fish biomass. Our results stress the paramount role of *Cystoseira brachycarpa* forest for coastal fish assemblages and emphasize the need to develop better management practices of human activities impacting *Cystoseira* spp. Moreover, considering the numerical importance of crypto-benthic fish, we advocate the combined use of UVC and AES for the future studies that will aim to draw a reliable picture of the whole coastal fish assemblage structure.

Box 1: Definition of necto-benthic and crypto-benthic fish used in the present study. Necto-benthic fish are species or life history stages of species that live associated to the sea bottom and remain most of the time in the water just above the substrate. They only seek in shelter (*e.g.* in cavity, crevasses, within vegetation) for limited periods, for instances when threatened by a predator, for resting or for breeding (Harmelin 1987). They are therefore conspicuous in the eyes of scuba diver performing UVC. Oppositely, crypto-benthic fish presently refer to all species or life history stages of species that remain most of the time upon or within the substrate and that are not easy to detect visually (Depczynski & Bellwood 2003) This definition of 'crypto-benthic' is pragmatic and refer to the 'hard to spot' nature of these fish, despite they may have various ecological relations with the substrate: *e.g.* very small epi-benthic fish (laid on the substrate), epi-benthic cryptic fish that use camouflage, truly crypto-benthic fish that spend most of their time sheltered (*e.g.* in a hole, among pebbles or within vegetation) (new terminology suggested by Kovačić *et al.* 2012). Despite this more ecologically meaningful terminology, we will use the 'hard to spot' sense of crypto-benthic since it pragmatically distinguishes fish reliably surveyed by an harvesting method (hereafter 'crypto-benthic') from fish reliably surveyed by UVC (the conspicuous 'necto-benthic').

1 Introduction

Habitat degradation is recognized as a major threat to terrestrial, aquatic and marine ecosystems (Chapin *et al.* 2000; Keith *et al.* 2013). This may affect ecological processes underlying abundances and distributions of organisms, community structures, the whole functioning of ecosystems, and their resistance and resilience. Ultimately, this may reduce ecosystems' potential to provide sustainably good and services to humans (Chapin *et al.* 2000; Folke *et al.* 2004; Cardinale *et al.* 2012).

In subtidal Mediterranean rocky reefs, *Cystoseira* species (Fucales), large canopy-forming brown algae, may form forest-like habitats called '*Cystoseira* forests' (Clarisse 1984). Most of *Cystoseira* species are sensitive to direct and indirect human impacts, and their regression has been recorded across the entire Mediterranean (Thibaut *et al.* 2005; Gianni *et al.* 2013) and is still ongoing. Depending on the identity and intensity of anthropogenic stressors, *Cystoseira* forests can (have) be(en) replaced by less structurally complex habitats. In areas with degraded water quality (*e.g.* increase in turbidity, waste waters, other pollutant), *Cystoseira* forests disappear(ed) and are (were) replaced by Dictyotales- , Sphacelariales- and/or articulated Corallinales- dominated assemblages (forming shrublands-like habitats or turfs depending on the replacing species)(Airoldi & Beck 2007; Mangialajo *et al.* 2008). In areas where date-mussel fishery and/or overfishing (especially of the sea breams) occur(ed), *Cystoseira* are (were) replaced by barren grounds (bare rocks with only encrusting coralline algae or invertebrates, hereafter called 'barren')(Guidetti *et al.* 2004; Guidetti 2006; Hereu *et al.* 2008).

Sala *et al.* (2012) did a basin-scale comparison of fish assemblage structure between these different states of the Mediterranean rocky reefs. They assessed algal, invertebrates and fish assemblages (at 8-12 m deep) in 32 localities all over the northern Mediterranean Sea (NW, North-central and NE) and identified 4 main community states: (1) inside the well-enforced marine reserves, ‘predator dominated’ ecosystem with large fish biomass and non-canopy algae, and (2 to 4) in lowly or unprotected localities, (2) ecosystems with lower fish biomass, but abundant algal canopies (including mainly *Cystoseira* sp.), (3) ecosystems with very low fish biomass and extensive barrens and (4) ecosystems with very low fish biomass and extensive algal turfs. The lower fish biomass in *Cystoseira* forests compared to the highest fish biomass in non-canopy algal habitats, was unexpected. Indeed, *Cystoseira* forest is generally considered as an ‘healthy’ state of rocky reefs that is expected to harbor high fish biomass. Sala *et al.* (2012) suggested this might be due to their design that encompassed mainly the 2 combinations of (1) non-canopy algal habitat inside well enforced marine reserve, and (2) *Cystoseira* forests in lowly or unprotected localities. This design was constrained by the fact that most of the well enforced marine reserve were established in localities that potentially suffered from historical decline of *Cystoseira* forests (Thibaut *et al.* 2005). The highest fish biomass in non-canopy algal habitats inside marine reserves, might therefore resulted from the fact that recovery of *Cystoseira* spp. may take longer than recovery of fish assemblages (*e.g.* in Medes Islands Marine reserve, Sala & Boudouresque 1997; Hereu *et al.* 2008), or even that *Cystoseira* spp. may not naturally recover due to lack of propagules subsidies (Mangialajo *et al.* 2012; Gianni *et al.* 2013).

Few other studies compared fish assemblage structure between *Cystoseira* forest and other habitat-types. They all highlighted the possible importance of *Cystoseira* forests for fish, at least for some fish taxa at some of their life stages. In Gulf of Trieste (Adriatic Sea), Orlando Bonaca & Lipej (2005) recorded (at 0.5-3 m deep) the highest fish species richness (including both necto- and crypto- benthic fish, however see below) in patches of *Cystoseira* spp. compared to various other habitat-types differing in substrate type and/or algal cover. However, as regards densities, no species was primarily associated to patches of *Cystoseira* spp.. In Cyclades Archipelago (Aegean Sea), studies found (at 3 m deep) a positive correlation between percent cover of *Cystoseira* spp. and densities of *Symphodus tinca*, *Symphodus mediterraneus*, and *Coris julis* (Giakoumi & Kokkoris 2013) but no correlation was detected when considering all fish taxa pooled (Giakoumi *et al.* 2012). In Corsica (Liguria Sea), Cheminée et al (2013) focused on juvenile fish of necto-benthic taxa and detected (at 2-4 m deep) higher densities of *Symphodus* spp. juveniles in patches of *Cystoseira* forests compared to patches of shrublands, the opposite for densities of *Coris julis* juveniles, and no difference for juveniles of other necto-benthic taxa including *Serranus* spp. juveniles.

All these studies used underwater visual census (UVC) for assessing fish assemblage structure in *Cystoseira* forest and other less structurally complex habitats. UVC has the main advantage of being non-destructive, and is particularly suitable for assessing necto-benthic fish (see Box 1 for definition), which are conspicuous (Harmelin-Vivien *et al.* 1985; Francour 1999; Murphy & Jenkins 2010). However, UVC is recognized to under-estimate richness and densities of crypto-benthic fish (see Box 1 for definition), which are 'hard to spot' especially in habitats that have complex architectural structure such as coral reefs or seagrass (Ackerman & Bellwood 2000; Willis 2001; Smith-Vaniz *et al.* 2006; Bozec *et al.* 2011). Consequently, by using UVC we may have a distorted picture of fish composition and density patterns, biased towards larger necto-benthic fish. It has to be considered that crypto-benthic fish assemblage structure is reliably assessed only by the use of an harvesting method (*e.g.* using anesthetic like Quinaldine or piscicide like rotenone: Jordan *et al.* 1997; Ackerman & Bellwood 2000; Willis 2001; Depczynski & Bellwood 2003; Smith-Vaniz *et al.* 2006; Bozec *et al.* 2011; Kovačić *et al.* 2012).

Kovačić *et al.* (2012) quantitatively and reliably compared crypto-benthic fish diversity and densities (using quinaldine in sampling area of fixed surface) among various Mediterranean habitat-types (from 1 to 20 m). Unluckily, *Cystoseira* forests were considered as absent from their study area (Kvarner area, Adriatic Sea). Other qualitative or falsely quantitative (by UVC) studies focused on crypto-benthic fish but they did not included *Cystoseira* forest (Patzner 1999; La Mesa *et al.* 2004; La Mesa *et al.* 2006), excepting one qualitative study that focused only on the 7 Mediterranean species of Gobioscidae (Hofrichter & Patzner 2000). All these studies highlighted that crypto-benthic fish are diversified and abundant in various subtidal habitats of the Mediterranean Sea. However, almost nothing is known on crypto-benthic fish assemblage in *Cystoseira* forests. This is detrimental because crypto-benthic fish may be highly abundant and putatively have an important role in the functioning (*e.g.* trophodynamic) of the ecosystem (Depczynski & Bellwood 2003).

The present study combined for the first time in NW Mediterranean Sea the use of (1) UVC for sampling necto-benthic fish and (2) enclosed anesthetic station (EAS) for sampling crypto-benthic fish, in order to compare the whole fish assemblage structure between *Cystoseira* forests, and the less structurally complex habitat-types Turf and Barren.

2 Material and Methods

2.1 Sampling sites

We sampled fish and macroalgae assemblages within 2 regions of the North-Western Mediterranean Sea, Corsica and Menorca (Figure 1). We sampled 10 sites in Corsica in May 2011 and 13 sites in Menorca in July 2011. We could not intersperse sampling times among the two regions, due to logistic constraints. Nevertheless, we collected all data during late-spring early-summer when the habitat structural complexity provided by macroalgae presents slow temporal variations, because this period coincides to the peak of macroalgal biomasses after spring growth (Hoffmann *et al.* 1992). Within each of the two region-time combinations, we sampled in two locality: one protected (within a Marine Protected Area, MPA) and one unprotected (outside Marine Protected Areas, OUT). This did not aim (nor allow) to assess putative protection effect. This was constrained by habitat distribution. Especially in Menorca-July, we found more sites presenting *Cystoseira* Forest in the protected locality (North-MPA), and we found sites presenting Turf only in the unprotected locality (East-OUT), despite we tried to balance the sampling design as much as possible (Figure 1). It is worth noting that putative variations between localities within a region, may be due to natural spatial variations and/or protection effects, which could not be discerned.

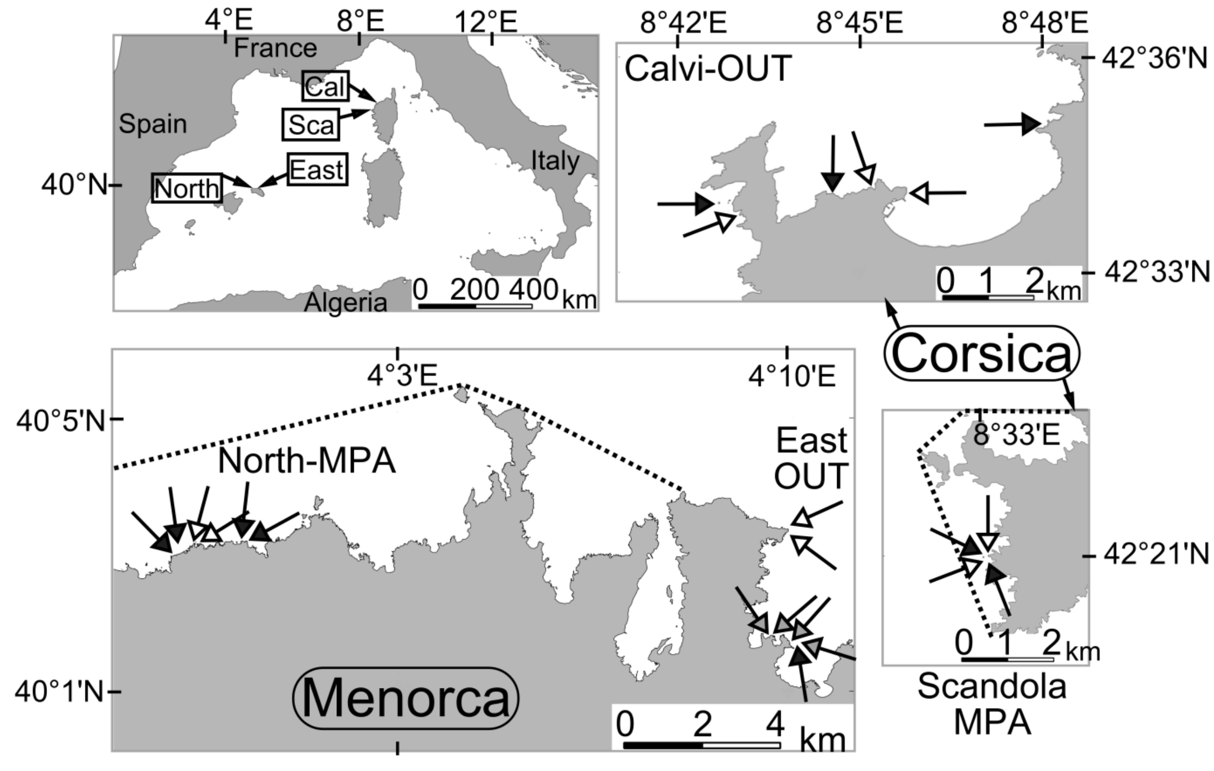


Figure 1. Localization of the sampled sites. Black filled arrows are forest sites, white filled arrows are barren sites, grey filled arrows are turf sites. 'Sca' and 'Nor' localities were within the Marine Protected Areas (MPA) 'Scandola Marine Reserve' and 'Norte de Menorca Marine Reserve', respectively. Dotted lines indicate MPA boundaries. The 2 other localities were outside (OUT) marine reserve.

Within each locality, we selected sampling sites by visual inspection of both abiotic features and macroalgal cover. We tried to find an equal number of sites for each of the 3 targeted habitat-types, which differed only in terms of macroalgal assemblage since abiotic features were controlled due to their possible effects on fish assemblage structure (*e.g.*: Letourneur *et al.* 2003). Specifically, *criteria* in regard to abiotic features were: an area at least 900 m², between -4 m and -9 m depth, presenting only monolithic rock (as opposed to blocks, pebbles etc.), with gentle slope (0° to 15°), and low substrate rugosity (*i.e.* steps, crevasses and overhang were avoided). *Criteria* in regard to macroalgal assemblage were: at least 80% of the 900 m² 'abiotic-controlled' area must be covered by one of our 3 targeted habitat-types. Surfaces of our sampling sites were site small, but larger areas fulfilling all the above mentioned *criteria* are usually difficult to find in Subtidal Mediterranean rocky reefs.

2.2 Data collection

2.2.1 Ethic statements

The experimental harvesting protocol by scuba-diving was approved by 'Direction interrégionnale de la mer Méditerranée' (the French administration in charge of the Maritime affairs in Corsica), and by 'Direccio General de Pesca, Govern de Illes Balears' (the Spanish administration in charge of the Maritime affairs in Menorca). After fish collection, all efforts were made to minimize pain when killing fish, by using anesthesia (quinaldine) overdose, following the Directive 2010/63/EU of the European Parliament and of the Council.

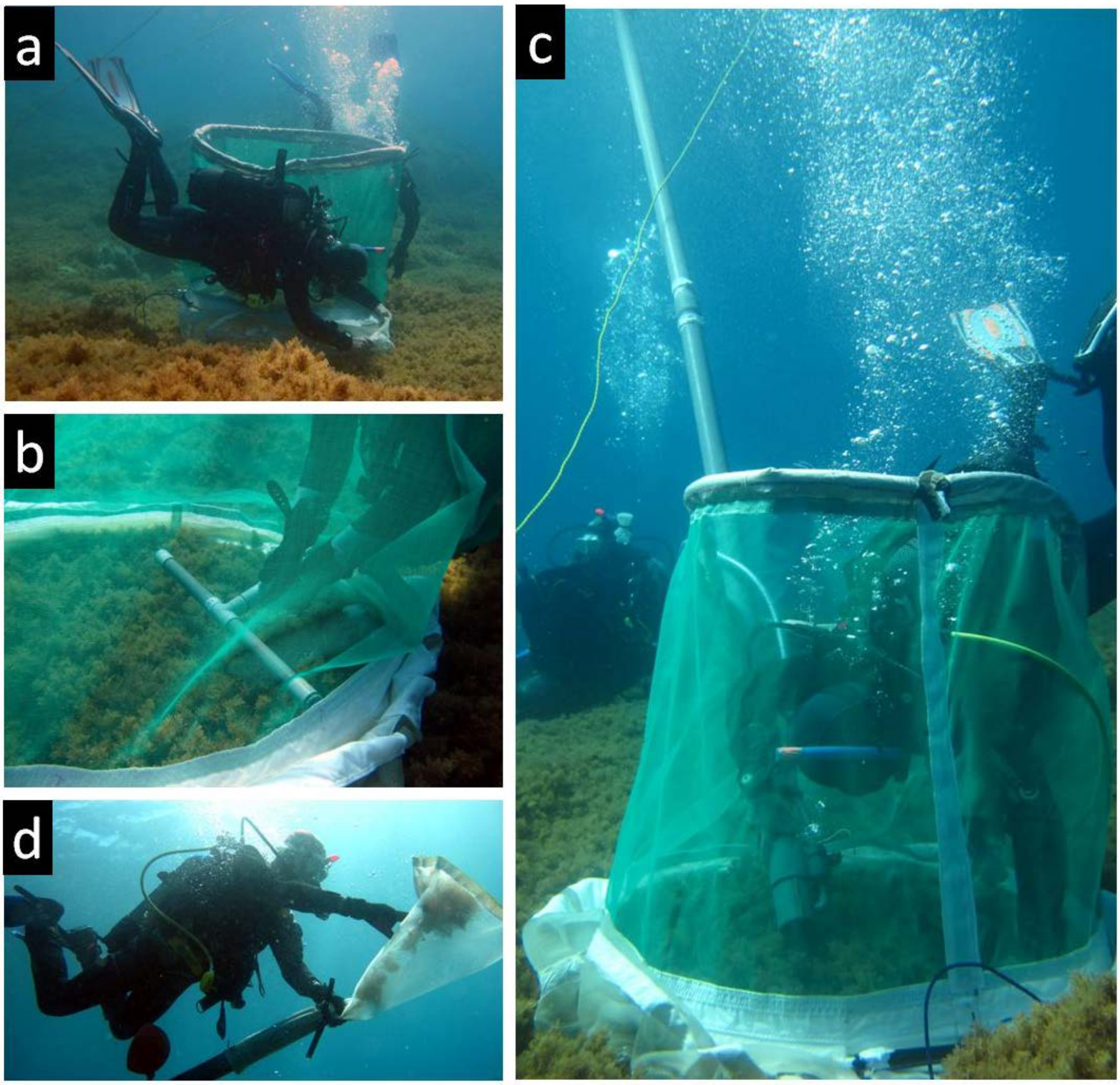
2.2.2 Macroalgae Assemblage

We sampled biomasses of macroalgae in order to *a posteriori* verify that our sampled sites (visually selected) were appropriately grouped into meaningful habitat-types, and to describe them more precisely. By scuba-diving, we scraped (using chisel and hammer) all non-encrusting macroalgae in three replicate 25 x 25 cm² quadrats at each sites. Each sample (algae from one quadrat) was placed in an individual zip-lock bag. After the dive, algal samples were individually removed from their bags, wrapped into a terrycloth impregnated with 70% alcohol, packed again in an hermetic bag, and stored in a cooler until we reached our field laboratory where we stored samples in a fridge. Algal biomass was measured within 3 days after collection. Water and alcohol excess from samples were removed using a salad spinner (30 seconds). Samples were individually sorted and weighed using operational taxonomic units (Table S1). Since we aimed to characterize fish habitat-types, algal biomass was pooled into the 6 following functional groups prior data analyzes: canopy-forming algae (mostly *Cystoseira brachycarpa* var. *balearica*, with sometimes less than 5% of *C. compressa* or *Sargassum* sp.), large erect algae (*e.g. Dictyota* spp.), small erect algae (*e.g. Acetabularia acetabulum*), turf-forming articulated corallinales, turf-forming filamentous algae, massive algae (i.e. *Codium bursa*).

2.2.3 Crypto-benthic fish assemblages

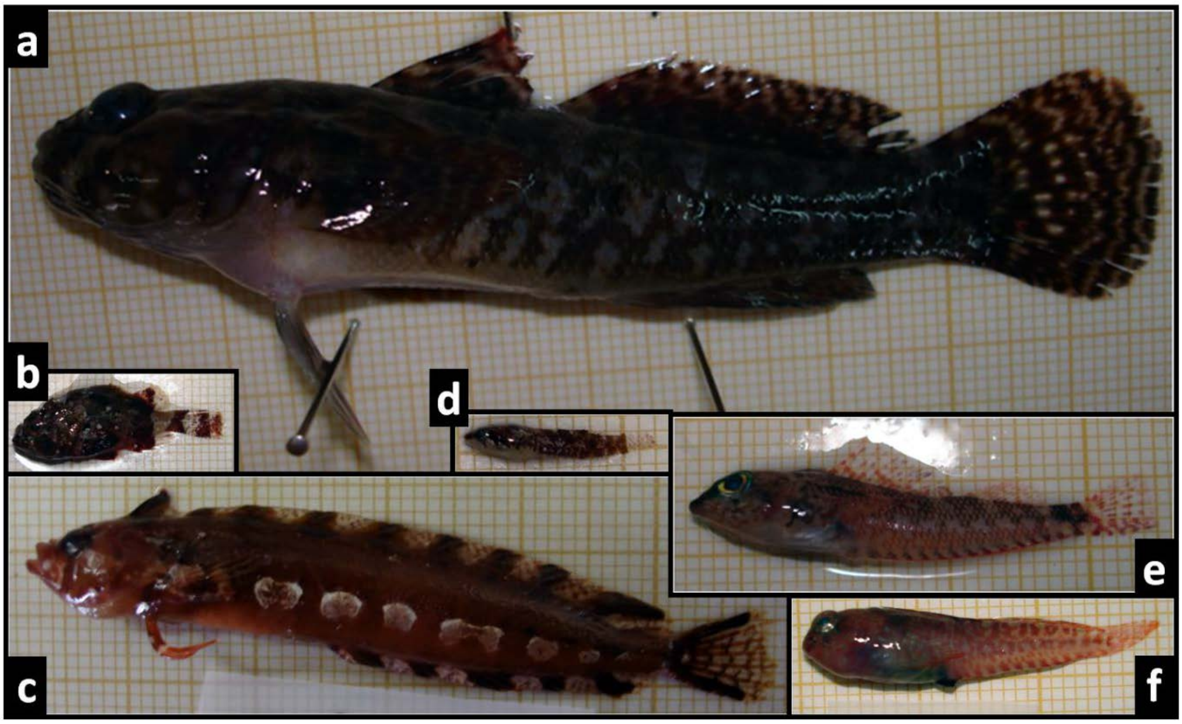
Crypto-benthic (CB) fish assemblage structure was assessed using an harvesting method. During daylight (10AM - 4PM), we conducted at each site 3 replicates of 1m² 'Enclosed Anesthetic Station' (EAS). The 1m² sample area was enclosed by a cage and sampled using fish anesthetic and air-lift pump (Photos panel 1). The cage was a cylinder, 0.56 m in radius, 1 m in height, without bottom nor roof in order to operate on the sea floor passing by the top of the cage, while preventing fish from escape. The circular wall of the cage was composed by a

1 mm mesh nylon fence mounted on a metal hoop. There was an extra tissue strip 0.25 m wide all around the base of the cage (like a skirt) with galvanized chain at its perimeter, so that the base could be molded to the substrate. Two scuba divers dropped the cage from 2 m above the seafloor. As soon as the cage touched the seafloor, one diver make sure the base of the cage (the 'skirt') was molded to the substrate and the second diver sprayed 2 L of anesthetic solution (1 cl of quinaldine, 10 cl of acetone, 189 cl of seawater) 15 cm above the substrate (Kovačić *et al.* 2012). One minute later, fish were collected by vacuuming using an air-lift pump (with a 1mm mesh collecting bag). The pump head was moved all around the 1 m² sample area during 1 min. As soon as the vacuuming session ended, the collecting bag was closed, and a new one was set-up for the next replicate.



Photos panel 1: some steps of the crypto-benthic fish sampling: a) Setting-up the 'skirt' of the cage ; b) Spraying of the anesthetic ; c) Vacuuming by air-lift ; d) Closing the collecting bag.

After the dive, every fish EAS samples (Photos panel 2) were individually stored in plastic tubes filled with 70% alcohol. In the laboratory, samples were individually sorted and every fish individuals were measured (nearest mm), weighed (nearest mg), and identified using binocular when necessary. Since many fish individuals were early juveniles (settlers) hardly recognizable until the species level, we identified every individuals to the family. Both Crypto-Benthic (CB) and Necto-benthic (NB) fish species were captured by EAS. NB fish were removed from the CB fish dataset for preventing overlap between CB and NB fish datasets. Early juveniles (settlers) of some NB fish species were kept in the CB dataset (and removed from the NB dataset) since they have a crypto-benthic behavior. Hereafter, for individuals belonging to a NB species, 'CBS' refer to the early juveniles that are at the Crypto-Benthic Stage, and 'NBS' refer to late juveniles and (sub-) adults that reached the Necto-Benthic Stage. A body-size threshold was used for discriminating CBS from NBS (see Table 3 in 'Results').



Photos panel 2: Some crypto-benthic fish collected using the 'Enclosed Anesthetic Station'. a) *Gobius paganellus ;* b) *Scorpaena* sp. * ; c) *Clinitrachus argentatus* ; d) *Lepadogaster* sp. *; e) *Tripterygion delaisi* ; f) *Parablennius* sp. * ; individuals marked with * are early juveniles. Backgrounds: 1 mm grid papers.

2.2.4 Necto-benthic fish assemblages

Necto-benthic fish data were collected using standard underwater visual (UVC) techniques (Harmelin-Vivien et al, 1985), modified for small sized resident NB fish (Cheminée *et al.* 2013). During daylight (10AM - 4PM), we conducted at each site 6 replicates of 9 m² point-snapshot-count. The random 9m² sample area was mentally visualized by the diver who stopped swimming randomly. The area was the half disk 2.5 m in radius (9.8 m²) in front of the diver. However, the inner part of this area (half disk 0.7 m in radius, 0.8 m²) was ignored because of its immediate vicinity with the diver. Within this 9m² area, the diver estimated body size (total length to the nearest 0.5 cm for fish ≤ 5cm, to the nearest 1 cm for larger fish) and species of every fish individuals that were present at the time the diver stopped swimming. Fish data were memorized in one shot (< 30 sec) and then written on a slate. Individuals of relatively mobile species (*e.g. Diplodus* sp.) were counted first for avoiding movement-induced biases. Shoaling and/or planktivorous species (*e.g. Chromis chromis, Oblada melanura, Sarpa salpa*) were not considered, as well CB species and CBS individuals that were sometimes visible in bare habitat. Fish biomasses were estimated using existing Length Weight Relationship from the literature (Morey *et al.* 2003; Froese & Pauly 2012).

2.3 Data analysis

Sites were the key observational sampling units and were used as statistical sampling units. Indeed, every single site was the common denominator of the three database related to algae, CB and NB fish. Densities (and biomasses) were averaged over replicates and mean values (for each site) were stated in individuals (and grams) per 10 square meter. This enabled to bind the matrices of CB and NB fish data for getting a unique site x fish taxa matrices. Using sites as statistical units did not affect the analysis of variances when comparing inter-habitat (group of sites) variability over intra-habitat variability (Murtaugh 2007).

2.3.1 Habitat-types

Biomasses of the 6 algal functional groups were analyzed to verify *a posteriori* that our sampled sites were appropriately grouped into meaningful habitat-types. Objectively-defined groups of sites were obtained by running the PRIMER routine combining (group-average) hierarchical clustering and Type 1 SIMPROF test, on Bray-Curtis dissimilarity matrices with square root transformed data (Clarke *et al.* 2008; Somerfield & Clarke 2013).

2.3.2 Fish assemblages

To analyze the effects of habitat-type on multiple aspects of fish assemblage structure, 9 multivariate descriptors were considered, combining 3 sets of fish category (all fish, only crypto-benthic fish, only necto-benthic fish) and 3 types of metrics (presence/absence, densities, biomasses). Jaccard similarity was used on presence/absence. Bray-Curtis dissimilarity was used on square root transformed densities and biomasses. Similarly, nine univariate descriptors were also used: number of taxa, total density and total biomass for each of the 3 sets of fish category.

To test putative differences between Forest and Barren for each of these (multivariate or univariate) descriptors of fish assemblage structure, we used 3 ways permutational (multivariate or univariate) analyses of variance (PERMANOVAs): the factor Region-Time ('RT', fixed, 2 levels: Corsica-May and Menorca-July), the factor Locality-Protection ('LP', fixed, 2 levels nested within each 'RT' level), the factor Habitat-type ('HA', fixed, 2 levels: Forest, Barren). The habitat Turf was excluded from the ANOVA design because Turf sites were sampled only within the locality East-OUT, and consequently this would have induced empty cells in the design. The design was unbalanced, we therefore used both Type I and Type III sum of squares (SS). For the sake of space, we reported only Type III SS, but we did look at the type I SS with terms included in all possible orders, to confirm inferences. The factors RT and LP were fixed. This enabled to assess the effects of habitat-type separately for each of the four localities and then averaging these effects. Treating RT and LP as random factors would not be appropriate, since it would be equivalent to draw inferences about the whole of the NW Mediterranean for the whole of the summer (of just 2011) from just four points (localities), which are a mix of space, time and protection level. Univariate PERMANOVA were based on Euclidian distance which makes this non parametric test the equivalent of a parametric ANOVA but free from the assumption of normality of residuals (Anderson & Millar 2004). Appropriate post-hoc pair-wise comparisons were used when necessary. P-values were obtained by 9999 permutations of residuals under a reduced model.

To identify groups of fish taxa whose density responded in a similar way to the differences detected between habitat-types and between region-time (the two only factors affecting significantly multivariate densities, see 'Results'), Type 2 and Type 3 SIMPROF were used. These methods are analogous to Type 1 SIMPROF, excepting that taxa are clustered rather than sites, simply by transposing the 'site X taxa' matrix. Type 2 SIMPROF tested the null hypothesis of 'no associations among taxa'. Type 3 SIMPROF intended to identify statistically distinct groups of taxa, by combining (group-average) hierarchical clustering of taxa and Type 2 Similarity Profile Test (Somerfield & Clarke 2013). Only taxa that occurred in at least 4 out of the 23 sites were considered, since the method is sensitive to the inclusion of the most rare taxa (Somerfield & Clarke 2013). The Index of associations was used on standardized densities ('by total') previously averaged over the combined factor Habitat x Region-Time. This methodological approach had the twofold advantage of grouping taxa by broad patterns and controlling experimentwise type I error rate, over the alternative not recommended approach consisting in a series of univariate tests (taxa per taxa) for putative differences in density between habitat-types.

To visualize multivariate patterns, Metric-Multidimensional Scaling (MDS) were used on the 3 dissimilarity matrices involving all fish taxa. To get a faithful visualizations of dissimilarities in 2D ordinations, we used only centroids of the combined factor Habitat x Locality-Protection (Region-Time).

Body-size (total length) distributions of all Crypto-benthic and all Necto-Benthic fish individuals (pooled separately) were visualized in order to (1) better understand their relative contribution into total density and total biomass, (2) visualize putative differences among habitats. A smoothed histogram (Kernel Density Estimation) was plotted for each level combinations of Habitat x Locality-Protection (Region-Time). For each histogram, the Kernel Density Estimation was computed on body-size of all fish individuals pooled. At this stage, the surface below the Kernel Density curve represents 1. Kernel Density Estimations were multiplied by the total fish abundance averaged over sample, in order to plot the count curve whose the surface below represents the averaged fish density.

All SIMPROF tests and PERMANOVAs were performed using the PRIMER 6 and PERMANOVA + B20 package (Clarke & Gorley 2006; Anderson *et al.* 2008). All graphical visualizations were performed in R Environment (R Development Core Team 2013) using the libraries vegan (Oksanen *et al.* 2012) and ggplot2 (Wickham 2009).

3 Results

3.1 Habitat-Types

Biomasses of the 6 algal functional groups were not homogeneous among sites (Similarity Profile Test, $\pi = 2.186$, $p = 0.02$). The combined clustering/SIMPROF analysis delimited 3 groups of sites significantly different from each other, but internally homogeneous. This objective clustering confirmed our *a priori* visual selection of sampling sites. Habitat-type of each site is displayed in Figure 1. Mean macroalgal assemblage structure of each habitat-type is presented in Figure 2. The habitat-type Forest exhibited the highest total biomass. It was clearly dominated by Fucales (> 90% of total macroalgal biomass were *Cystoseira brachycarpa* var. *balearica*) that formed a dense canopy (around 15 to 20 cm in height). The habitat-type Turf exhibited lower total biomass (70% of the Forest's biomass). It was dominated by Erect articulated Corallinales. They formed a dense layer of turf (around 10 cm thick) that smothered few short-sized individuals of Fucales. Some small and large erect algae were sparsely covering the turf layer. The habitat-type Barren exhibited very low total biomass (10% of the Forest's biomass). In some sites, few short-sized individuals of Fucales (< 5cm) and of erect algae (mostly *Padina* sp.) were scattered.

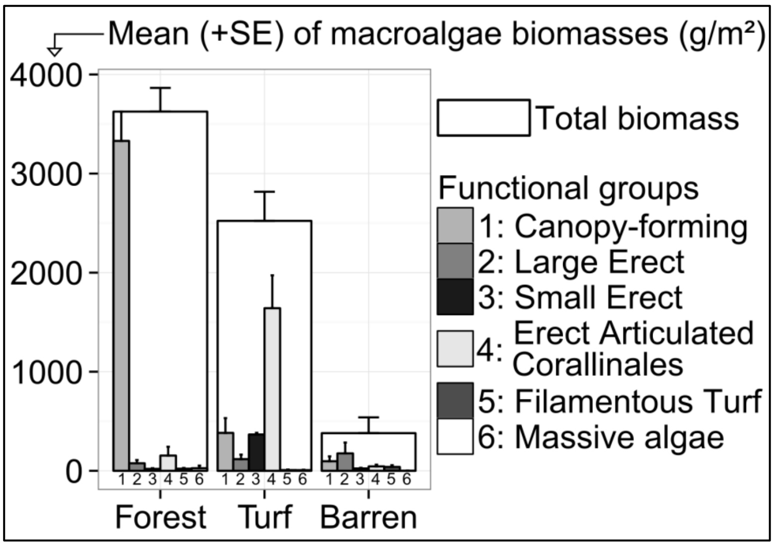


Figure 2. Macroalgae assemblage structures in the 3 habitat-types. Mean total biomass (+SE) of macroalgae and mean biomasses (+SE) of the 6 macroalgal functional groups.

3.2 Univariate descriptors of fish assemblage structure

Number of taxa of (1) all fish, (2) only crypto- and (3) only necto-benthic fish were significantly different between the habitat-types Forest and Barren (PERMANOVAs, Table 1). Mean values of all 3 variables were higher in Forest (Figure 3). There were also some variations between regions-times. The number of taxa of (1) all fish and (2) only crypto-benthic fish were both significantly higher in Menorca-July than in Corsica-May, irrespectively of the habitat-type (Table 1 and Figure 3). For (3) the number of taxa of necto-benthic fish, differences between regions-times were less clear cut (term RT close to the significance threshold, Table 1). This was due to the variability between the 2 localities within the regions-times (term LP(RT) significant, Table 1). In regard to the habitat-type Turf (not included in PERMANOVAs, see M&M section), its mean number of all fish taxa (as well both CB and NB taxa subsets) seemed similar to those recorded in the Barren sites of the same locality (East).

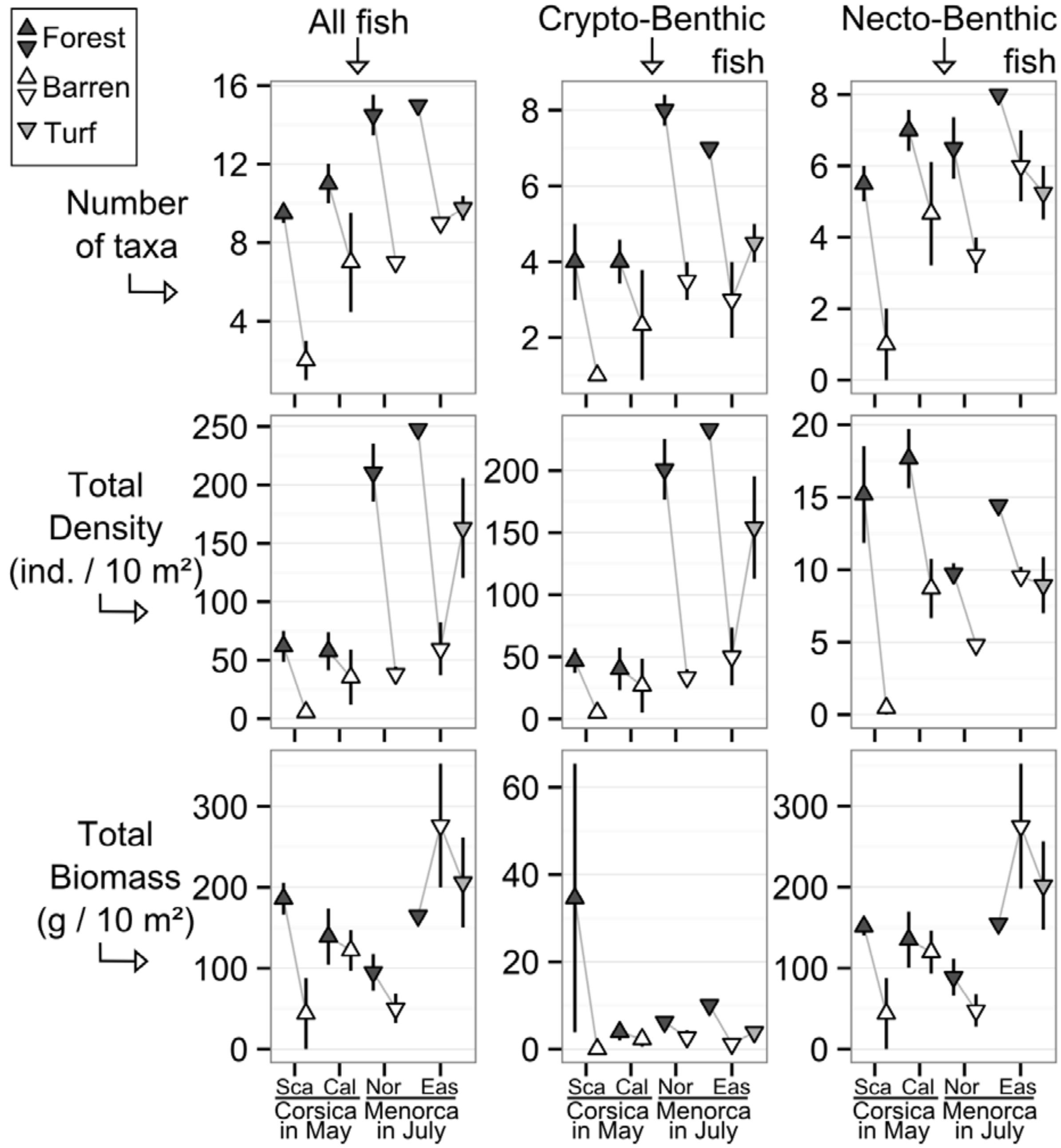


Figure 3. Univariate descriptors of fish assemblage structures among habitat-types and regions-times. Mean values (+/- SE) of the number of taxa (observed per site), the total density and the total biomass, for each Habitat x Locality-Protection (Region-Time) levels combinations.

The total densities of crypto-benthic fish were in average 11 times higher than the total densities of necto-benthic fish. This explained why total density of all fish broadly followed the pattern of crypto-benthic fish density (Table 1 and Figure 3). Crypto-benthic fish density, and consequently all fish density, responded significantly to the interaction region-time x habitat-type (Table 1). Pairwise comparisons evidenced significant differences between Forest and Barren within Menorca-July (Table 1), with higher density in Forest (Figure 3). Within Corsica-May, no difference was detected between habitat-types (Table 1). Necto-benthic fish density showed a different pattern. It also responded significantly to the interaction region-time x habitat-type (Table 1), but within both regions-times, necto-benthic fish densities were significantly higher in Forest than in Barren (Table 1 and Figure 3), with the Forest-Barren difference more pronounced within Corsica-May (Figure 3). Concerning the habitat-type Turf, mean crypto-benthic fish density, and consequently all fish density, seemed intermediate in Turf between the low mean density of Barren and the high mean density of Forest recorded in the same locality (East). Contrastingly, mean necto-benthic fish density in Turf seemed similar to the one in Barren (Figure 3).

The total biomasses of necto-benthic fish were in average 5 times higher than the total biomasses of crypto-benthic fish. This explained why total fish biomass followed broadly the pattern of necto-benthic fish biomass (Table 1 and Figure 3). None of the 3 total biomass variables (all fish, only crypto- and only necto-benthic) showed significant difference between habitat-types (Table 1). The main source of variation (other than residual variations) in the necto-benthic fish biomass (and consequently in all fish biomass) was the locality-protection within region-time (term LP(RT) significant, Table 1) and the interaction region-time x habitat-type in a lesser extent (term RT x HA close to the significance threshold, Table 1). This was probably due to the locality East that had in average higher necto-benthic fish biomass compared to the 3 other localities, along with an opposed trend in Forest-Barren differences (Figure 3). Concerning crypto-benthic fish biomass, none term was significant in the PERMANOVA (Table 1). However, graphical visualizations might suggest a trend with higher biomass in Forest than in Barren, which could have been masked by the large variability among Forest sites of the locality Scandola (Figure 3).

Table 1. Results of PERMANOVAs on univariate descriptors of fish assemblage structure in Forest and Barren. RT: Region-Time; HA: Habitat-Type; LP: Locality-Protection. ns not significant; ° $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

		All fish			Crypto-benthic fish			Necto-benthic fish		
Source	**df**	**SS**	**F**		**SS**	**F**		**SS**	**F**	
Number of taxa										
RT	1	65.4	**12.08**	**	26.4	**13.72**	**	8.7	3.33	°
HA	1	159.6	**29.50**	***	44.3	**23.00**	***	35.8	**13.72**	**
LP(RT)	2	28.1	2.60	ns	2.1	0.54	ns	23.1	**4.44**	*
RTxHA	1	1.0	0.19	ns	3.8	1.95	ns	0.9	0.33	ns
LP(RT)xHA	2	8.4	0.77	ns	1.2	0.31	ns	3.3	0.63	ns
Residual	11	59.5			21.2			28.7		
Total density										
RT	1	399.7	**31.77**	***	406.8	**33.81**	***	0.0	0.43	ns
HA	1	492.8	**39.16**	***	420.5	**34.95**	***	2.9	**39.54**	***
LP(RT)	2	19.2	0.76	ns	12.1	0.50	ns	1.1	**7.49**	**
RTxHA	1	203.0	**16.13**	**	223.5	**18.57**	**	0.5	**6.77**	*
LP(RT)xHA	2	8.1	0.32	ns	5.9	0.25	ns	0.2	1.38	ns
Residual	11	138.4			132.7			0.8		
Pairwise tests		Corsica: t = 2.05 °			Corsica: t = 1.50 ns			Corsica: t = **5.27** **		
Forest *vs* Barren		Menorca: t = **5.86** **			Menorca: t = **5.70** ***			Menorca: t = **5.51** **		
Total biomass										
RT	1	23.5	0.76	ns	1.1	0.62	ns	34.7	1.11	ns
HA	1	21.8	0.70	ns	6.0	3.42	ns	4.9	0.16	ns
LP(RT)	2	395.3	**6.38**	*	4.9	1.38	ns	404.5	**6.48**	*
RTxHA	1	130.6	4.22	°	1.5	0.82	ns	104.6	3.35	°
LP(RT)xHA	2	202.1	3.26	°	6.6	1.88	ns	166.7	2.67	ns
Residual	11	340.7			19.4			343.0		

3.3 Body-size distributions

Concerning the differences in body-sizes between crypto-benthic and necto-benthic fish, most of crypto-benthic fish were smaller than necto-benthic fish irrespectively of the habitat-type (Figure 4). Specifically, more than 75% of crypto-benthic fish individuals were smaller than 25 mm (3rd quartile < 25 mm in boxplots Figure 4), excluding the Forest sites of the locality Scandola (Corsica-May) where the 3rd quartile approached 35mm due to the presence of some larger individuals (until 95mm). Contrastingly, all necto-benthic fish individuals were larger than 25 mm. More than 75% of necto-benthic fish individuals were larger than 50 mm, excluding the Forest sites of Menorca-July where a great proportion of fish sized between 25 and 50 mm was recorded. Through the positive correlation between body-weight and body-size, the overall larger sizes of necto-benthic fish explained the dominance of necto-benthic fish in terms of biomass despite the dominance of crypto-benthic fish in terms of densities (see previous section and Figure 3).

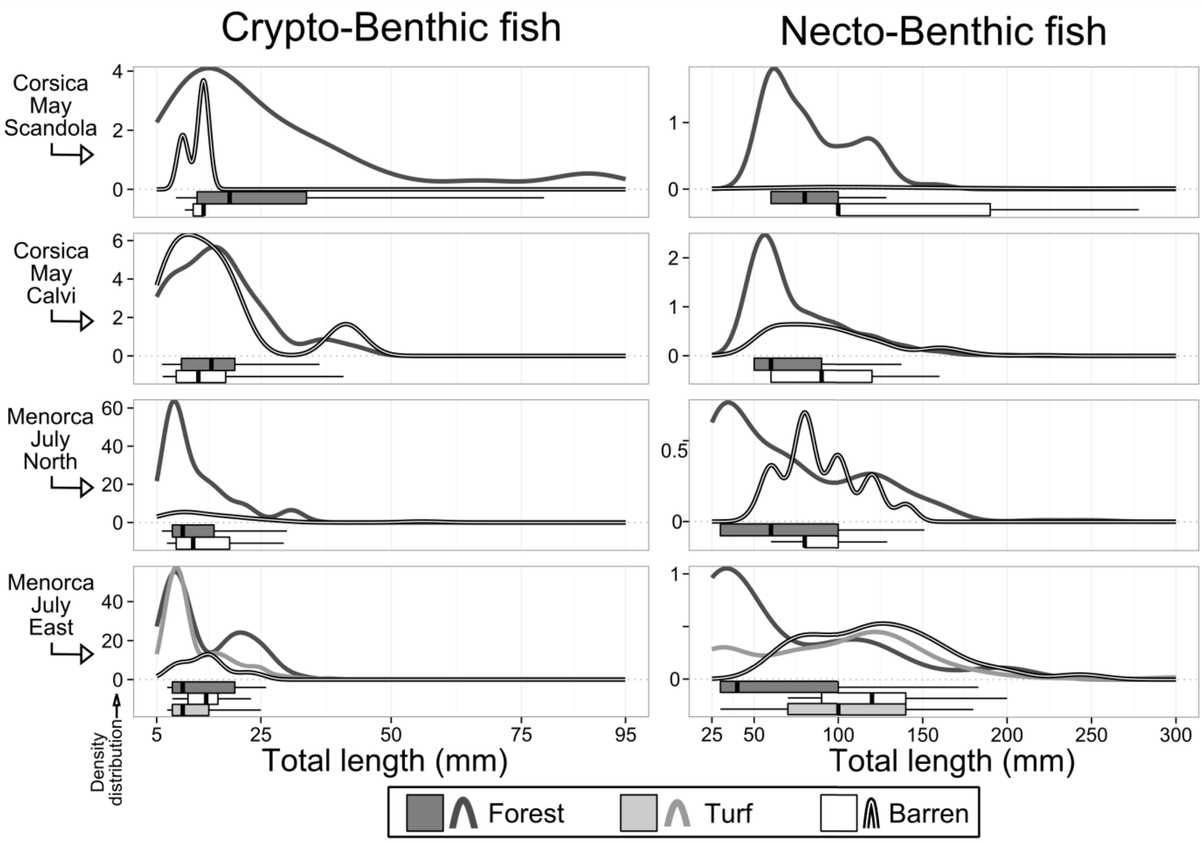


Figure 4. Smoothed histograms of fish body-size among habitat-types and regions-times. The surfaces below the curves (Kernel density estimations) indicate the total fish abundance averaged over sample units.

Concerning differences between habitat-types in crypto-benthic fish body-size distributions, patterns were not consistent between the 4 localities. This was mainly due to large variability among Barrens compared to the relative consistency among Forests. Nevertheless, in 3 out 4 localities (excluding Calvi), the curve (smoothed histogram indicating fish density as a function of their body size, Figure 4) of Forest never crossed the curve of Barren and was always above. This indicated that fish were more abundant in Forest, irrespectively of their body size. In the fourth locality Calvi, curves of Forest and Barren followed the same trend indicating that density (seen in Figure 3) and body-size were similar. Focusing on the locality East of Menorca-July (the only one where it had been possible to sample the Turf Habitat), the Turf curve was superimposed to the Forest curve from 5 to 15 mm and was below further, due to a second mode in the Forest curve around 20 mm. This indicated that very small individuals (5 to 15 mm) are as abundant in Forest as in Turf, while larger individuals (especially those sized around 20 mm) were more abundant in Forest.

Concerning differences between habitat-types in necto-benthic fish body-size distributions, patterns were also inconsistent between region-times. In Corsica-May, the forest curve was above the Barren curve in both locality, indicating higher fish densities of all sizes in forests. In Menorca-July, the Forest curve was above the Barren curve from 25 to 70 mm, indicating higher densities of small-sized (25 to 70 mm) fish in Forest. From 70 mm, trends were different between the two locality. In North, fish sized between 70 and 120 mm were more abundant in Barren, and fish between 120 mm and 200 mm were slightly more abundant in Forest. In East, fish larger than 120 mm (until the largest observed at 300 mm) were more abundant in Barren (especially those sized around 130 mm). Concerning Turf (only in East), densities of fish sized between 25 and 70 mm were intermediate between the low one of Barren and the high one of Forest. From 70 mm, size distribution of Turf curve followed the same trend than Barren (similar curve shape) but indicated lesser densities (curve positioned below).

Synthetically, the higher fish densities in Forest compared to Barren were mainly due to small fish individuals that were abundant in Forest and almost absent in barren (especially for necto-benthic fish). The higher densities in Forest of Menorca-July compared to Forest of Corsica-May were mainly due to the very-small fish individuals that were highly abundant in Forests of Menorca-July (for both crypto- and necto-benthic fish).

3.4 Multivariate descriptors of fish assemblage structure

Results of PERMANOVAs analyses of the 9 multivariate descriptors of fish assemblage structure are reported in Table 2. Multivariate patterns were significantly different between the habitat-types Forest and Barren, and between the region-time Corsica-May and Menorca-July, irrespectively of the multivariate descriptor considered among the 9 analyzed. This evidenced that (1) the differences in the whole fish assemblage structure were due to both the subsets of crypto- and necto-benthic fish, and (2) the differences in (subsets of) fish assemblage structure were in terms of taxa composition as regards the 3 descriptors using Jaccard similarity, and possibly also in terms of abundances and biomasses as regards the 6 descriptors using Bray-Curtis dissimilarity. Some differences between localities within regions-times were detected on the biomasses of necto-benthic fish, and consequently also on biomasses of the whole fish assemblage but this did not significantly interact with Habitat-Type nor with Region-Time effects.

Table 2. Results of PERMANOVAs on multivariate descriptors of fish assemblage structure in Forest and Barren. RT: Region-Time; HA: Habitat-Type; LP: Locality-Protection. ns not significant; ° p < 0.1; * p < 0.05; ** p < 0.01; *** p < 0.001.

		All fish			Crypto-benthic fish			Necto-benthic fish		
Source	**df**	**SS**	**F**		**SS**	**F**		**SS**	**F**	
Composition (Jaccard)										
RT	1	7428.1	**5.23**	***	6140.4	**5.06**	**	7296.3	**6.02**	***
HA	1	7334.8	**5.17**	***	4254.2	**3.50**	*	9762.7	**8.06**	***
LP(RT)	2	3296.0	1.16	ns	1022.6	0.42	ns	3809.2	1.57	ns
RTxHA	1	2056.1	1.45	ns	2626.2	2.16	°	997.2	0.82	ns
LP(RT)xHA	2	3570.9	1.26	ns	1508.7	0.62	ns	4356.3	1.80	°
Residual	11	15613.0			13359.0			13332.0		
Composition and Densities (Bray-Curtis on square root transformed data)										
RT	1	7498.9	**5.96**	***	7209.2	**6.81**	***	5860.0	**7.18**	***
HA	1	5139.7	**4.08**	**	4389.9	**4.14**	*	8452.9	**10.36**	***
LP(RT)	2	3023.3	1.20	ns	1076.5	0.51	ns	3456.5	2.12	°
RTxHA	1	2872.2	2.28	°	2369.0	2.24	°	1598.7	1.96	ns
LP(RT)xHA	2	3177.1	1.26	ns	1354.1	0.64	ns	3640.2	2.23	°
Residual	11	13849.0			11652.0			8977.9		
Composition and Biomasses (Bray-Curtis on square root transformed data)										
RT	1	6475.2	**6.62**	***	5491.8	**2.70**	*	6576.4	**7.13**	***
HA	1	5621.5	**5.75**	***	6097.4	**2.99**	*	5629.7	**6.10**	***
LP(RT)	2	5776.4	**2.96**	**	3036.8	0.75	ns	5685.4	**3.08**	***
RTxHA	1	2272.3	2.32	°	3810.9	1.87	°	2234.4	2.42	°
LP(RT)xHA	2	4075.9	2.09	°	2987.4	0.73	ns	4184.4	2.27	°
Residual	11	10751.0			22401.0			10149.0		

The MDS plot based on all fish presence/absence data (Figure 5-A) highlighted the clear additive effects (Table 2) of the factors Habitat-Type (along the 2nd axis) and Region-Time (along the 1st axis) on fish assemblage composition. In regard to the MDS plot based on all fish densities (Figure 5-B), differences between Barren and Forest (along the 2nd axis) appeared slightly higher in Menorca-July than in Corsica-May. This trend was also suggested by the interaction term Region-Time x Habitat-Type that was close to the significance threshold (0.1 < p < 0.05).

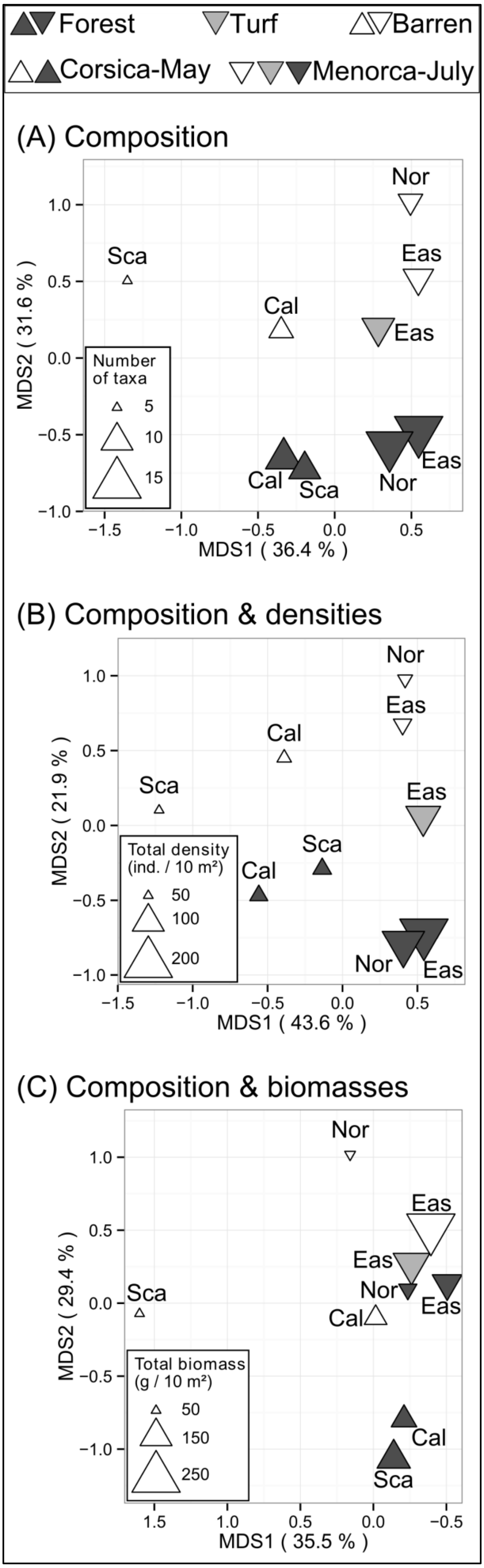


Figure 5. Multivariate descriptors of fish assemblage structures among habitat-types and regions-times. Metric-Multidimensional Scaling (MDS) plots (1st and 2nd axes, with % of explained variance between brackets) of centroids for the combined factor Habitat x Locality-Protection (Region-Time), performed on the matrices of (A) presence/absence data using Jaccard similarity, (B) square root transformed densities using Bray-Curtis dissimilarity, and (C) square root transformed biomasses using Bray-Curtis dissimilarity. Labels refer to the 4 Locality-Protection levels. See Figure 1, and M&M for more details.

In regard to the MDS plot based on all fish biomasses (Figure 5-C), multivariate differences between habitat-types and between region-times seemed to both occur in the same direction (mainly along the second axis on the 2D plot) and contrastingly to density, differences in biomass between habitat-types appeared less pronounced within Menorca-July.

Concerning the habitat-type Turf, which was sampled only in the locality East, in each MDS plots (Figure 5), the centroid of Turf x East was positioned between the centroids of Barren x East and Forest x East that were apart of each other. This was particularly pronounced on the MDS plot based on abundances (Figure 5-A), while on the MDS plot based on biomass, the 3 points were closer to each other (Figure 5-B). This suggested multivariate differences, at least in terms of composition and abundances. Hence, structure of Turf fish assemblage (of the few sites sampled in locality East) might be an intermediate between the clearly distinct structures of Forest and Barren fish assemblages, especially in terms of taxa composition and abundances.

3.5 Groups of taxa varying similarly

The Type 2 SIMPROF test rejected the null hypothesis of 'no associations among species' (π = 0.043, p = 0.021). Type 3 SIMPROF identified 6 groups of taxa that were significantly different from each other, but internally homogeneous, in terms of their trends in density variations across habitat-types and regions-times. The group 4 split in two subgroups 4a and 4b when significance threshold was set at 0.1 (instead of 0.05). This distinction was retained because ecologically meaningful (see group descriptions below). Variations are displayed on a common scale (standardized density) in Figure 6. Densities and body-size of each taxa are reported in Table 3.

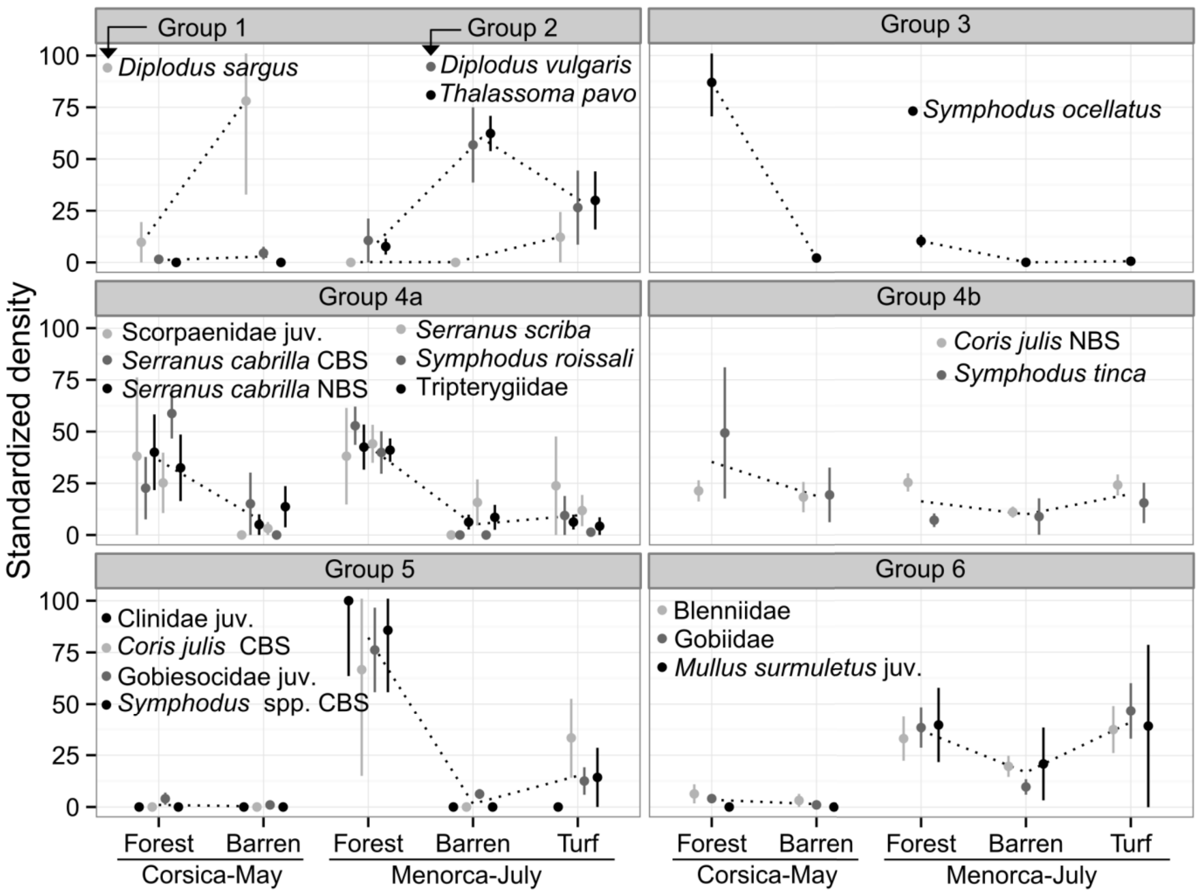


Figure 6. Groups of taxa varying similarly across habitat-types and regions-times. Mean standardized density (+/-SE) indicates variations of every taxa on a common scale, despite their respective densities may be greatly different. CBS: crypto-benthic stages of necto-benthic species (*i.e.* juveniles); juv.: taxa whose only juvenile individuals were recorded. See Table 3 for detailed information about body-size and absolute densities of each taxa.

Groups 1 and 2 were composed by necto-benthic species that were more abundant in Barren sites but species were segregated by regions-times. *Diplodus sargus* (group 1) was recorded almost only in Barren sites of Corsica-May. *Diplodus vulgaris* and *Thalasoma pavo* (group 2) were recorded almost only in Menorca-July, with higher abundances in Barren, intermediate in Turf, and lower in Forest.

Group 3, 4a and 5 were in average more abundant in Forest sites in at least one region-time. The necto-benthic *Symphodus ocellatus* (group 3) was highly abundant in forests of

Corsica-May and was also abundant in forests of Menorca-July, while almost never recorded in Barren and Turf irrespectively of the region-time.

Group 4a was the larger and more diversified group, composed of both crypto- and necto-benthic fish, sized from 1 to 24 cm (Table 3). They were more abundant in Forest and rarely observed in other habitats, consistently across regions-times.

Group 4b was composed by the labrids *Coris julis* and *Symphodus tinca* that were ubiquitous. They were recorded in every habitats-types of both regions-times. The trend of slightly higher density in Forest (especially for *S. tinca*) explained the proximity of groups 4a and 4b in the clustering.

Group 5 was composed essentially by crypto-benthic juvenile fish, belonging to crypto-benthic taxa (Clinidae and Gobioscidae juveniles) and necto-benthic taxa (early juveniles of *Coris julis* and *Symphodus* spp. at the crypto-benthic stage, CBS). They were almost strictly recorded in Menorca-July (excepting Gobioscidae) where they were more abundant in Forest than in Turf and almost absent from barren. Concerning the few individuals of Gobioscidae recorded in Corsica-May (relatively to the other region-time, Table 3), they were more abundant in Forest.

Group 6 was composed by crypto-benthic fish belonging to the family Bleniidae and Gobiidae and the necto-benthic *Mullus surmuletus* (only small sized individuals, see Table 3). They were less abundant in Corsica-May (M. *surmuletus* was even absent) than in Menorca-July. Within Menorca-July, they were recorded in every habitats (with many juveniles of Gobiidae and Blennidae in a lesser extent, see density and mean size in Table 3) with densities higher in both Forest and Turf compared to Barren. Concerning the few individuals of Bleniidae and Gobiidae recorded in Corsica-May, they were more abundant in Forest (Table 3).

Table 3. Groups of taxa varying similarly across habitat-types and regions-times. G: groups delimited by Type 3 SIMPROF test (See also Figure 6); N: Necto-benthic fish sampled by UVC; C: Crypto-benthic fish sampled by Enclosed Anesthetic Station. CBS: Crypto-benthic stages of necto-benthic species.

G	Family	Taxa		Size range, mm	Mean Size (SE)	Mean densities (SE) (indiv. / 10 m²)				
						Corsica-May		Menorca-July		
						Forest	Barren	Forest	Barren	Turf
1	Sparidae	*Diplodus sargus*	N	[80,300]	144 (20.2)	0.04 (0.04)	0.3 (0.17)	-	-	0.05 (0.05)
2	Labridae	*Thalassoma pavo*	N	[50,160]	92.7 (3.1)	-	-	0.3 (0.15)	2.41 (0.33)	1.16 (0.54)
2	Sparidae	*Diplodus vulgaris*	N	[60,160]	109.5 (3.4)	0.04 (0.04)	0.11 (0.07)	0.26 (0.26)	1.39 (0.44)	0.65 (0.44)
2	Total 2					0.04 (0.04)	0.11 (0.07)	0.56 (0.38)	3.8 (0.77)	1.81 (0.67)
3	Labridae	*Symphodus ocellatus*	N	[30,120]	59.8 (1)	7.52 (1.42)	0.19 (0.19)	0.89 (0.26)	-	0.05 (0.05)
4a	Labridae	*Symphodus roissali*	N	[25,150]	70.6 (3.2)	1.96 (0.4)	-	1.33 (0.34)	-	0.05 (0.05)
4a	Scorpaenidae		C	[15,43]	29 (5.1)	1.33 (1.33)	-	1.33 (0.82)	-	0.83 (0.83)
4a	Serranidae	*Serranus cabrilla* CBS	C	[12,32]	20 (2.1)	2 (1.33)	1.33 (1.33)	4.67 (0.82)	-	0.83 (0.83)
4a	Serranidae	*Serranus cabrilla*	N	[35,180]	94.9 (6.7)	0.59 (0.27)	0.07 (0.07)	0.63 (0.16)	0.09 (0.05)	0.09 (0.05)
4a	Serranidae	*Serranus scriba*	N	[60,240]	135.3 (6.8)	0.3 (0.17)	0.04 (0.04)	0.52 (0.11)	0.19 (0.13)	0.14 (0.09)
4a	Tripterygiidae		C	[13,56]	20.2 (1)	12.67 (6.27)	5.33 (3.89)	16 (2.21)	3.33 (2.36)	1.67 (1.67)
4a	Total 4a					18.85 (6.69)	6.78 (5.18)	24.48 (2.53)	3.61 (2.36)	3.61 (1.29)
4b	Labridae	*Coris julis*	N	[25,250]	88.9 (1.8)	4.96 (1.19)	4.26 (1.7)	5.89 (1.02)	2.55 (0.62)	5.6 (1.18)
4b	Labridae	*Symphodus tinca*	N	[35,300]	126.6 (9.3)	1.04 (0.67)	0.41 (0.28)	0.15 (0.07)	0.19 (0.19)	0.32 (0.21)
4b	Total 4b					6 (1.01)	4.67 (1.93)	6.04 (1)	2.73 (0.75)	5.93 (1.31)
5	Clinidae		C	[10,23]	17.9 (1.7)	-	-	4.67 (1.7)	-	-
5	Gobiesocidae		C	[5,14]	8 (0.2)	2.67 (1.94)	0.67 (0.67)	50.67 (13.6)	4.17 (1.6)	8.33 (4.41)
5	Labridae	*Coris julis* CBS	C	[15,21]	18.7 (0.8)	-	-	3.33 (2.58)	-	1.67 (0.96)
5	Labridae	*Symphodus* spp. CBS	C	[7,20]	10.4 (1.1)	-	-	10 (3.5)	-	1.67 (1.67)
5	Total 5					2.67 (1.94)	0.67 (0.67)	68.67 (10.98)	4.17 (1.6)	11.67 (4.19)
6	Blenniidae		C	[15,43]	21.5 (1)	2.67 (1.94)	1.33 (1.33)	14 (4.52)	8.33 (2.15)	15.83 (4.79)
6	Gobiidae		C	[7,95]	13.9 (0.6)	10.67 (3.4)	2.67 (1.94)	101.33 (25.55)	25.83 (9.85)	122.5 (35.26)
6	Mullidae	*Mullus surmuletus*	N	[50,100]	75 (2)	-	-	0.7 (0.32)	0.37 (0.31)	0.69 (0.69)
6	Total 6					13.33 (4.94)	4 (2.45)	116.04 (28.85)	34.54 (8.56)	139.03 (39.24)

4 Discussion

By combining the use of underwater visual census (UVC) and enclosed anesthetic station (EAS), we compared for the first time in Mediterranean rocky reefs, the structure of the whole (both crypto- and necto-) benthic fish assemblage between the endangered structurally complex habitat *Cystoseira brachycarpa* forest (Hoffmann *et al.* 1992) and the less structurally complex habitat-type Barren and Turf.

4.1 Richness and total density of crypto- and necto-benthic fish

4.1.1 Crypto-benthic fish, an important compartment often neglected

The total densities of crypto-benthic fish represented in average 92 % of total fish densities. On the contrary, the total biomasses of crypto-benthic fish represented in average 17 % of total fish biomass, due to the overall larger sizes of necto-benthic fish. The large dominance of crypto-benthic fish in terms of densities emphasis their potential importance in rocky reefs ecosystem functioning, despite their low biomass. Some studies suggested that static biomass estimates do not adequately reflect the rapid turnover and high productivity of these small sized crypto-benthic fish, which are (1) small-sized crypto-benthic fish taxa which typically have shorter life cycles (Depczynski & Bellwood 2003; Depczynski & Bellwood 2005) or (2) crypto-benthic juveniles of necto-benthic taxa that settle, growth and recruit into the necto-benthic assemblage in few months (Félix-Hackradt *et al.* 2014). These small sized individuals are herbivores (Blenniidae) and micro- or meso- carnivores (others Family, depending on body-size) and they may be prey items for various larger invertebrates and fish (Harmelin-Vivien *et al.* 1989; Stergiou & Karpouzi 2002). Crypto-benthic fish may consequently be important trophodynamic pathways (Ackerman & Bellwood 2000; Depczynski & Bellwood 2003). Results of the present study stress the need to consider crypto-benthic fish that were largely ignored until now, and advocate the combination of UVC and EAS for achieving a reliable picture of the whole fish assemblage structure (Ackerman & Bellwood 2000; Smith-Vaniz *et al.* 2006).

4.1.2 Broad patterns between habitat-types

Multivariate patterns of both crypto- and necto-benthic fish assemblage structures were different between *Cystoseira brachycarpa* forest and Barren (and maybe turf), consistently among the two regions-times. Necto-benthic fish were more diversified and more abundant in forests of the two regions-times. Crypto-benthic fish were more diversified in forests of both regions-times, but were significantly more abundant in forests only in Menorca-July, although a similar but not significant pattern was detected in Corsica-May. Orlando-Bonaca and Lipej (2005) found similar results as regards the high diversity of both crypto- and necto- benthic fish in *Cystoseira* forests. However, they did not detect higher densities in *Cystoseira* forest compared to the other various habitat-types they sampled. Giakoumi *et al.* (2012) also did not detected higher fish densities in *Cystoseira* forest. This might be related to the fact they used UVC and may consequently have underestimated crypto-benthic fish densities especially in *Cystoseira* forest, the most complex habitat where small fish can remain hidden below the canopy. Another non-exclusive explanation may be due to the fact that both studies used a correlative approach by sampling fish along gradients of both abiotic and biotic habitat features. The various habitats compared were therefore different in terms of algal cover but also in terms of depth, substrate nature and rugosity (*e.g.* rock, boulders, pebbles, sand), implying that they could not disentangle the respective effects of each habitat features. In the present study, the most important abiotic features affecting fish assemblage (substrate nature and rugosity, depth, slope)(Ruitton *et al.* 2000; Letourneur *et al.* 2003; Consoli *et al.* 2008) were controlled in our sampling design. The observed differences in fish assemblage structure between habitat-types were solely due to the effects of macroalgae, and this evidenced the paramount role of the canopy-forming *Cystoseira brachycarpa* for both juvenile and adult fish belonging to various taxa (see below).

Our results corroborate the worldwide broad patterns of higher fish diversity and density in vegetated habitats compared to adjacent un-vegetated habitats (or at least structurally less complex). Examples include seagrasses compared to adjacent bare sediments (Guidetti 2000, Bostrom *et al.* 2006, Horinouchi *et al.* 2009, Schultz *et al.* 2009, Schultz & Kruschel 2010), mangrove roots compared to adjacent mud flats (Laegdsgaard & Johnson 2001, Manson *et al.* 2005, Nanjo *et al.* 2011), giant kelp forests compared to adjacent bare rocks (Jones 1984, Anderson & Millar 2004), rocky reefs covered by non-canopy erect algae compared to bare rocks (Guidetti *et al.* 2004). This broad patterns is also recognized in terrestrial ecosystems where diversity and densities of numerous invertebrates and vertebrates taxa are correlated with structural complexity of plant assemblages (studies on arthropods, reptiles, amphibians, birds and mammals reviewed by Tews *et al.* 2004).

The effects of macrophyte on fish density and distribution patterns may rely on their two functions, primary producer and habitat-formers (Heck & Orth 1980, previous and next chapters of this manuscript). Macrophytes may provide fish with both food (directly and indirectly through primary and secondary consumers)(Connolly 1994) and shelter (*e.g.* interstitial space between roots, trunks, leaves)(Bartholomew & Shine 2008). Food and shelter availability may affect directly density patterns through starvation- and predation-induced mortality (*e.g.* Hindell *et al.* 2000, more details in previous and next chapters of this manuscript). Food and shelter availability may also affect prey and predator decision making in terms of habitat selection, which may affect density patterns through net migration (*e.g.* Horinouchi *et al.* 2013, more details in previous and next chapters). Therefore, the association of some (numerous) fish taxa (or of some life history stages of taxa, such as juvenile stage) with *Cystoseira* forest and the association of some others (more scarce) taxa with barren, may depend upon their life history traits such as feeding habits and morphological and behavioral anti-predation strategies. We will therefore discuss in the next paragraphs the possible factors that determined the observed taxa-specific density patterns, lightened by their life history traits founds in the literature.

4.2 Fish associated to *Cystoseira* forests

4.2.1 Consistent patterns across region-times

Fish taxa that were more abundant (or only present) in forests consistently across regions-times were taxonomically and functionally diversified. It included the crypto-benthic fish Trypterygidae (diurnal, eggs and invertebrates feeders, Stergiou & Karpouzi 2002), Scorpaeniade (nocturnal sit-and-wait macrocarnivores, invertebrates and fish feeders, Harmelin-Vivien *et al.* 1989) and *Serranus cabrilla* crypto-benthic juveniles, and the necto-benthic fish *Serranus* sp. (sub)-adults (diurnal stalck-and-attack macrocarnivores, invertebrates and fish feeders,Viladiu *et al.* 1999; Stergiou & Karpouzi 2002; Alos *et al.* 2011), *Symphodus roissali* and *S. ocellatus* (diurnal invertebrates feeders, Stergiou & Karpouzi 2002). The ubiquitous *Coris julis* (diurnal invertebrates -sea urchins included-feeders, Stergiou & Karpouzi 2002; Guidetti 2007) was also present in high abundance.

These density patterns observed for *Symphodus* spp. juveniles and adults corroborate with previous studies on *Cystoseira* forest (Cheminée *et al.* 2013; Giakoumi & Kokkoris 2013). Other studies also highlighted Trypterygidae and *Symphodus* spp's preference for habitats with erect algae in regions where *Cystoseira* forest were not present (Garcia Rubies & Macpherson 1995; Ruitton *et al.* 2000; Letourneur *et al.* 2003; La Mesa *et al.* 2004). Contrastingly, the presently observed higher densities of *Serranus* spp. in forests were more surprising, since some studies found that their densities were not affected by the structure of algal assemblage (La Mesa *et al.* 2002; Cheminée *et al.* 2013).

The coexistence of both small (prey) fish and macrocarnivores (in part piscivores) fish in *Cystoseira* forest might be due to lower (starvation- and/or predation- induced) mortality in forest and/or habitat selection (immigration). Whatever, the association of prey fish to the predator-rich forest might be related to the fact that prey may escape predation thanks to the forest canopy (see next chapter), which may overcome the higher (compared to barren) encounter rates with predators (Lima 1992). Higher densities of their food resources (invertebrates) in *Cystoseira* forest compared to barren (Chemello & Milazzo 2002; Gozler *et al.* 2010) may be also a determining factor. Macrocarnivores association to forest, on the other hand, may be linked to higher prey densities. Both invertebrates (see above) and small-sized fish (Cheminée *et al.* 2013, the present study) are more abundant in *Cystoseira* forests. This may overcome the possible negative effect of habitat structure on macrocarnivores foraging efficiency (Lannin & Hovel 2011). Moreover, foraging strategy that involves almost no predator movements, such as sit-and-wait (and stalk-and-attack in a lesser extent), may be unaffected by habitat structure (Schultz & Kruschel 2010) or may be favored (Rilov *et al.* 2007). Lastly, macrocarnivores may be prey of higher order predators such as *E. marginatus* and *D. dentex*. From this perspective, the structural complexity provided by *Cystoseira* sp. may reduce the strength of prey-predator lethal interactions at every trophic levels (at least few individuals may always survive) and consequently promotes persistence of populations forming a diversified faunal community associated to *Cystoseira* forest (Janssen *et al.* 2007).

4.2.2 Variability between regions-times

Fish were more abundant in forest of Menorca-July and this was mainly due to higher abundances of very small sized individuals, such as new settlers of Gobioscidae, Clinidae, Blenniidae, Gobiidae, *Coris julis* (CBS), *Symphodus* spp. (CBS). Density increase due to arrival of new settlers along the warm season (from late spring to autumn) had been documented for these crypto-benthic taxa (Beldade *et al.* 2006; Felix-Hackradt *et al.* 2013) and necto-benthic taxa (Lejeune 1985; Raventos & Macpherson 2005; Cheminée 2012; Cheminée *et al.* 2013; Felix-Hackradt *et al.* 2013). From these perspectives, the patterns we observed were likely due to seasonal variability (or at least spatio-temporal) rather than consistent spatial variability between regions, despite our sampling design did not allow to disentangle this two sources of variability. This stresses the importance of sampling several times (during different seasons) when assessing fish assemblages, especially in nursery habitats such as *Cystoseira* forests (Cheminée *et al.* 2013).

4.3 Fish associated to Barren

The only taxa showing higher densities in Barren than in Forest were *Diplodus sargus* (in Corsica-May), and *D. vulgaris* and *Thalasoma pavo* (in Menorca-july). The ubiquitous *Coris julis* (CBS excluded) was also in high abundance in Barren in both regions-times. These species are the 4 most important sea urchin feeders in Mediterranean rocky reefs (Guidetti 2007 and references therein). Their presence in barrens (that are maintained by sea urchins) might be linked to foraging activity. However, their densities were probably insufficient for controlling sea urchin population and allowing recovery from barren state (Guidetti & Sala 2007). Concerning the independence of these larger taxa upon algal refuges, this might be related to their larger body-size (compared to fish associated to forest) that provides relative safety against predation ('refuge in size', *e.g.* Olson 1996).

Concerning the few Blenniidae and Gobiidae recorded in barren compared to forest, their presence may be due to the presence of some clumps of algae that could have been enough for sheltering. The presence of holes in the substrate may had also provided shelter. Parravicini *et al.* (2008) evidenced a positive correlation between number of holes and densities of Bleniidae. Kovačić et al (2012) also recorded some Blenniidae and Gobiidae species associated to bare rocks. He defined these species as 'epi-benthic' since they were not hidden below or within a physical structure, but rather used crypsis with susbtrate.

4.4 Fish associated to Turf

The few sites of Turf we sampled (only in Menorca-July) suggested that the new settlers of Blenniidae and Gobiidae had similar densities in Turf and Forest and lower in Barren. The structural complexity of the turf layer was very high, providing only very small interstitial space. The turf layer might be accessible to the very small sized settlers and explain their presence, while the turf layer might be less accessible or impenetrable to larger-sized individuals, such as those recorded in higher densities in forest than in turf or only in forest. In regard to the 4 sea urchin feeders that had intermediate densities in Turf, between Forest (low) and Barren (high), the impossibility to hide within the turf layer was maybe not a limiting factor (since it is also impossible to hide in barren where they were more abundant). Therefore, maybe lower food resources (or at least lower accessibility to resources due to physical constraints, see previous chapter) might be a more determining factor.

4.5 Limitations of the sampling design and possible solutions

Our conclusions, broadly *Cystoseira brachycarpa* forest host higher diversity and density of small-sized fish, are restricted to day-time, during early summer, on rocky reefs of low abiotic structural complexity (*e.g.* presenting no boulders nor crevasses). Day-night changes in fish assemblage structure had been reported in Mediterranean Sea for some nocturnal macro-carnivores such as Scorpaenidae, morey eels (*Murena helena*) and conger eels (*conger conger*) (Bell & Harmelin-Vivien 1982; Harmelin 1987). They may migrate inside prey-rich vegetated habitats, such as Posidonia meadows or *Cystoseira* forests, only at night or during sunrise and sunset, while during the day they remain in adjacent habitats rich in cavity for resting. The planktivorous damselfish *Chromis chromis* are also known to have dial migration between the water column occupied at day and the algal beds of cavity occupied at night (Azzurro *et al.* 2007). Seasonal variations in fish assemblage structure are also important in Mediterranean Sea. Fish have usually one reproductive period per year, and consequently pulses in densities of settlers and recruits are on a yearly basis (Lejeune 1985; Raventos & Macpherson 2005; Beldade *et al.* 2006; Felix-Hackradt *et al.* 2013). Also, adult fish of some species may reduce their activity during the cold season, and some species may have seasonal migrations (REFS). Abiotic habitat features were controlled in the present study. Our conclusions are therefore restricted to monolithic rocky reefs between 5 and 10 m deep, presenting low substrate complexity and gentle slope. Higher substrate rugosity (*e.g.* presence of boulders, cavity, crevasses) may positively affects fish species composition and densities, (Charton & Ruzafa 1998; Ruitton *et al.* 2000; Letourneur *et al.* 2003; Consoli *et al.* 2008; Bussotti & Guidetti 2009; Giakoumi & Kokkoris 2013).

Another limitation of the present study is related to its sampling design that was constrained by the segregated distribution of the habitat types across the NW Mediterranean Sea. Due to the lack of historical data on fish assemblages before *Cystoseira* populations decreased, a Before After Control Impact approach was not possible. The previous studies and the present one used therefore a 'space for time' approach, by comparing fish between areas where *Cystoseira* spp. were still present and other areas where *Cystoseira* spp. were absent. In order to assess the effects of macroalgae on fish and limit the possible confounding effects of other factors (such as spatial variations), we used a nested design with habitat-types nested within localities. We had therefore to select localities where every habitat types were present. On the continental shores, rocky seascapes are dominated mainly by shrublands. Patches of subtidal *Cystoseira* forests are rare and cover only very small surfaces (patch of 5 x 5 m²). This is too small for most of fishes (*i.e.* smaller than their home range). This would have been irrelevant to study this landscape from an habitat perspective. We therefore selected both Corsica and Menorca, where rocky seascapes are dominated by *Cystoseira* forests, and alternate habitat-types, such as barren grounds, cover small to medium areas embedded within *Cystoseira* forest (*i.e.* patch of 30 x 30m²). These surfaces are still small but reasonable for at least studying small-sized resident fish individuals, although totally irrelevant for larger fish (*e.g.* grouper, dentex, sea bass). However, even for small-sized fish, movements across patches of habitat-types are expected to be important (*e.g.* through habitat selection). From this perspective, it would be valuable to compare only wide habitat units. This could be achieved only by the comparison of localities that present a different dominant habitat type (*e.g.* wide forest of Corsica and Menorca versus wide shrublands of continental shores). This would induce strong spatial variability. This could be compensated, by sampling many localities in the NW Mediterranean (each one dominated by one of the habitat of interest), in order to integrate/encompass regional variability. This should be done everywhere in the same time, on several occasions during the year, as regards the seasonal (or at least spatio temporal) variability. This seems hardly achievable by a single team, (international) collaboration would be necessary.

5 Conclusion

Both crypto- and necto- benthic juvenile and adult fish were more diversified and more abundant in the endangered habitat *Cystoseira brachycarpa* forest compared to less structurally complex habitat-type Barren and Turf. This stresses the paramount role of *Cystoseira brachycarpa* forest for coastal fish assemblages and emphasizes the need to develop better management practices of the human activities impacting *Cystoseira* spp. (Gianni *et al.* 2013). Meanwhile, some further field surveys would be valuable for deepening our knowledge of dial and seasonal variations, as well the effects of seascape composition and configuration (see previous chapter). For such field survey, we advocate the combination of underwater visual census and enclosed anesthetic station in order to achieve a reliable picture of the whole fish assemblage.

Supplementary Information available at the end of the chapter:

- Table S1. List of the operational taxonomic units and their functional groups

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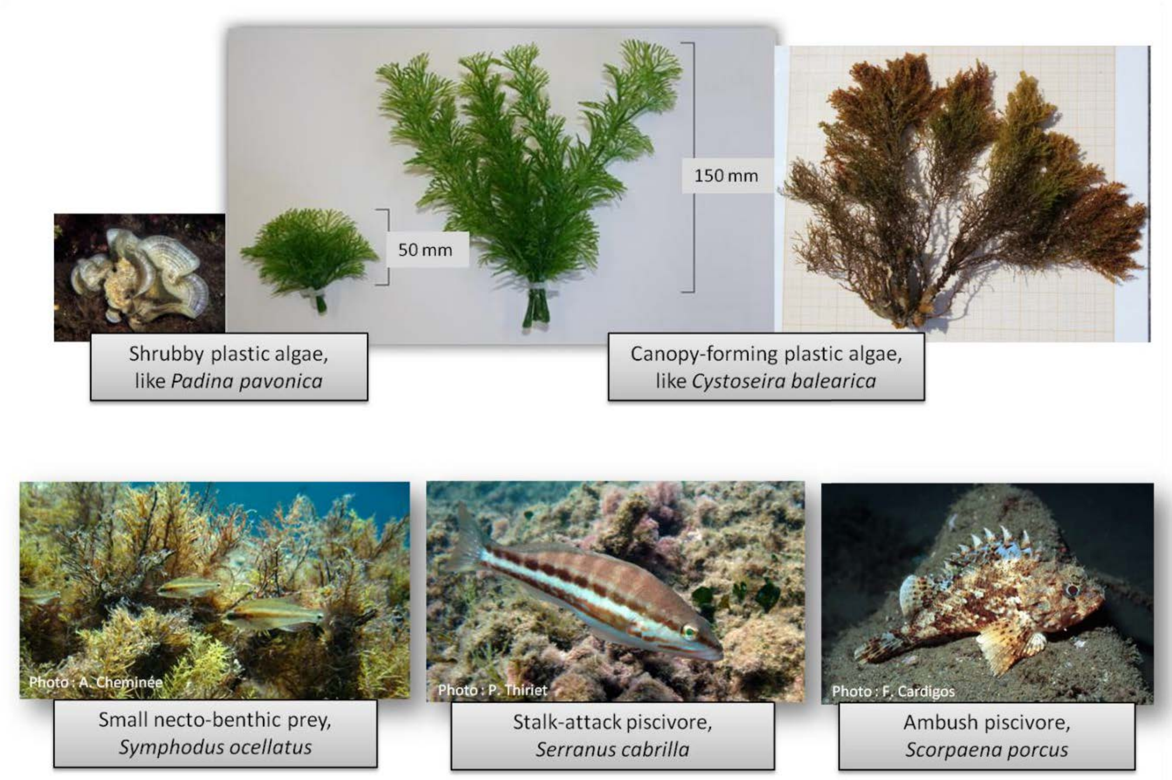
7 Supplementary Information

Table S1. List of the operational taxonomic units and their functional group

Operational taxonomic units	Functional groups
Cystoseira balearica	Canopy-forming Algae
Cystoseira compressa	Canopy-forming Algae
Sargassum spp.	Canopy-forming Algae
Dictyota intricata	Large erect algae
Dictyota faciola	Large erect algae
Halopteris scoparia	Large erect algae
Padina pavonica	Large erect algae
Dictyopteris polypodioides	Large erect algae
Digenea simplex	Large erect algae
Acetabularia acetabulum	Small erect algae
Anadyomene stellata	Small erect algae
Botryocladia spp.	Small erect algae
Caulerpa racemosa	Small erect algae
Dasycladus vermicularis	Small erect algae
Flabellia spp.	Small erect algae
Halimeda tuna	Small erect algae
Valonia spp.	Small erect algae
Amphiroa rigida	Turf-forming articulated Corallinales
Corralina elongata	Turf-forming articulated Corallinales
Jania rubens	Turf-forming articulated Corallinales
Other articulated Corallinales	Turf-forming articulated Corallinales
Laurencia complex	Turf-forming filamentous algae
Other green and red filamentous algae	Turf-forming filamentous algae
Codium bursa	Massive algae

Chapter 4. Fish prey-predator interactions mediated by habitat-forming algae: a tank experiment approach with Mediterranean rocky reef fish



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Abstract

Animal assemblages are usually more abundant and diversified within structurally complex habitats. In *Cystoseira* sp. marine forests (recognized as threatened habitats in the Mediterranean Sea), prey and predator fishes co-habit in higher densities, compared to other less complex habitats (*i.e.* shrublands or barren grounds). This may result, at least in part, from the effects of habitat complexity on prey-predator interactions. In order to investigate how habitat complexity mediates lethal and behavioral prey-predator interactions, we set up tank experiments, with the wrasse *Symphodus ocellatus* as model prey and the stalk-attacking comber *Serranus cabrilla* and the sit-and-wait scorpionfish *Scorpaena porcus* as model predators. Prey survival and adaptive anti-predator behavior were compared between 3 artificial habitats (forest, shrub, barren), and habitat selection of the 3 species was assessed. Wrasse survival face to each of the two predators increased with habitat complexity, and the increase in survival was more pronounced face to comber. Wrasse anti-predator behavior was predator-specific. Face to the comber, the wrasse sought refuge within vegetation (available only in shrub and forest). On the contrary, face to the scorpionfish, the wrasse increased its vertical distance from the predator, irrespective of the habitat structure. With regard to habitat selection, wrasse and comber chose the forest, independently of whether they were alone or together. The scorpionfish did not select any habitat, nor did the wrasse in scorpionfish's presence. Our results suggest that habitat complexity may affect fish habitat selection, and lethal and behavioral prey-predator interactions, with some predator-specific variations. In nature, higher fish densities in forest may be due, at least in part, to reduced mortality and/or net immigration of fishes into forest. Our findings further stress the important functional role of *Cystoseira* forests in Mediterranean coastal habitats and suggest that human-driven losses of *Cystoseira* forests may have negative effect on fish assemblage.

1 Introduction

Changes in environmental conditions (*e.g.* nutrient enrichment, global warming) may affect ecological processes underlying abundances and distributions of organisms, community structures, the whole functioning of ecosystems, and their resistance and resilience. Ultimately, this may reduce ecosystems' potential to provide sustainably good and services to humans (Chapin *et al.* 2000; Folke *et al.* 2004; Cardinale *et al.* 2012). Habitat degradation, including loss of habitat structure, is recognized as a major threat to ecosystems (Chapin *et al.* 2000; Keith *et al.* 2013) but the ecological processes that are specifically threatened remain poorly known (Gonzalez *et al.* 2011).

Habitat structure is defined as the amount, composition and three-dimensional arrangement of physical elements (both abiotic and biotic) at a location (McCoy & Bell 1991; Beck 2000; Byrne 2007). Abiotic elements shaping a habitat include mainly geo-morphological features (*e.g.* presence of boulders, crevasses, caves, overhangs) (Gimenez-Casalduero *et al.* 2011). Biotic elements include mainly plants in terrestrial systems (from grasses to trees), as well in benthic aquatic systems (seagrasses, mangrove roots), along with macroalgae (*e.g.* kelps) and sessile invertebrates (*e.g.* corals, oysters) (Thomsen *et al.* 2010).

Habitats with higher structural complexity (*e.g.* higher substrate rugosity or higher tree densities) usually harbor higher diversity and densities of animals, in terrestrial (studies of arthropodes, reptiles, amphibians, birds and mammals reviewed by Tews *et al.* 2004), freshwater (*e.g.* Gorman & Karr 1978 and references below) and marine (*e.g.* Alvarez-Filip *et al.* 2011 and next references) ecosystems worldwide. Focusing on aquatic vegetated habitats, numerous small-bodied fish (small species and juveniles) are more abundant within vegetated habitats compared to adjacent unvegetated habitats, which are structurally less complex. Examples include seagrasses compared to adjacent bare sediments (Guidetti 2000; Bostrom *et al.* 2006; Horinouchi *et al.* 2009; Schultz *et al.* 2009; Schultz & Kruschel 2010), mangrove roots compared to adjacent mud flats (Laegdsgaard & Johnson 2001; Manson *et al.* 2005; Nanjo *et al.* 2011), giant kelp forests compared to adjacent bare rocks (Jones 1984; Anderson & Millar 2004), *Cystoseira* forest compared to adjacent unforested habitats (Orlando Bonaca & Lipej 2005; Sala *et al.* 2012; Cheminée *et al.* 2013). Small-bodied fish inhabiting vegetated habitats, coexist with notably sit-and-wait (aka ambush) and stalk-and-attack piscivorous fishes (see previous references and Sheaves 2001).

The coexistence of prey and predatory fishes within vegetated habitats may be due to the presence of macrophytes, which are both primary producer and habitat-formers (Heck & Orth 1980). Macrophytes may provide fish with both food (directly and indirectly through primary and secondary consumers)(Connolly 1994) and shelter (*e.g.* interstitial space between roots, trunks, leaves)(Bartholomew & Shine 2008; Thiriet *et al.* 2014). Food and shelter availability may affect directly density patterns through starvation- and predation-induced mortality. Food and shelter availability may also affect prey and predator decision making in terms of habitat selection, which may affect density patterns through net migration. With regard to prey, shelter provided by vegetation may reduce predation mortality (*e.g.* Gotceitas & Colgan 1989; Hindell *et al.* 2000; Scharf *et al.* 2006; Nanjo *et al.* 2011), but it is quite difficult to generalize as the patterns depend on the species and systems considered. Other studies, in fact, highlighted a higher predation mortality in vegetated habitats that host sit-and-wait predators (*e.g.* Horinouchi 2007; Rilov *et al.* 2007; Horinouchi *et al.* 2009; Schultz & Kruschel 2010). Prey may also switch habitat depending on the identity of the predator, avoiding vegetated habitat possibly hosting sit-and-wait predators, but seeking refuge in vegetated habitats when threatened by a pursuit predator (aka chase attacker) (Savino & Stein 1989; Eklov & Persson 1996; Martin *et al.* 2010; Wirsing *et al.* 2010; Smith *et al.* 2011). Some prey have anti-predation behavioral strategy, such as shoaling, that may be efficient in unvegetated habitat face to pursuit predator (Horinouchi 2007). From the perspective of predators, higher prey densities in vegetated habitats may overcome the possible negative effect of habitat structure on predator foraging efficiency (Lannin & Hovel 2011). Moreover, foraging strategy that involves almost no predator movements, such as sit-and-wait (and stalk-and-attack in a lesser extent), may be unaffected by habitat structure (Schultz & Kruschel 2010) or may be favored (Rilov *et al.* 2007). Lastly, predators may be prey of higher order predators (*e.g.* large transient piscivorous fish) and may also benefit from 'sheltering effect'.

This large corpus of behavioral studies mainly focused on how prey/predator fish switch between vegetated and bare habitats in response to presence and identity of predator/prey. Prey-predator interactions within habitat remain poorly documented. Natural habitats extend on larger surfaces than the small surfaces typically used in experimental choice-arenas (Laurel & Brown 2006). In nature, fish may have to make decision within the habitat rather than across two distinct habitats (excepting if it is positioned at ecotone, Horinouchi 2007; Smith *et* *al.* 2011). The few studies dealing with fish anti-predator behavior within predator-rich structured habitats (*e.g.* in seagrass meadow: Laurel & Brown 2006; *e.g.* in coral reef: McCauley *et al.* 2010) highlighted that presence and identity of predator may affect prey vertical positioning. In these studies, structured habitats were composed by only two vertical strata: the structured stratum (seagrass leaves or coral) and the open-water stratum above. To our knowledge, prey-predator behavioral interactions have never been studied within a forest-like marine habitat, *i.e.* an habitat containing three vertical strata: 1) the above open-water stratum; 2) the canopy stratum of high structural complexity (branches); 3) the below understory stratum of lower structural complexity (main axis).

In Mediterranean rocky reefs, *Cystoseira* species (Fucales), large canopy-forming brown algae, may form forest-like habitats called '*Cystoseira* forests' (Clarisse 1984). Most of *Cystoseira* species are sensitive to direct and indirect human impacts, and their regression has been recorded across the entire Mediterranean (Thibaut *et al.* 2005; Gianni *et al.* 2013). Depending on the identity and intensity of anthropogenic stressors, *Cystoseira* forests can be replaced by less structured habitats, such as shrublands (Dictyotales- and Sphacelariales-dominated assemblages, hereafter called 'shrub') and/or barren grounds (bare rocks with coralline algae, hereafter called 'barren')(Guidetti *et al.* 2004; Guidetti 2006; Airoldi & Beck 2007; Mangialajo *et al.* 2008). Processes underlying the co-existence of abundant prey and predator fishes in *Cystoseira* forests compared to other less structurally complex habitats (shrubs and barrens) are mostly unexplored.

In this study, we set-up tank experiments using artificial algae, in order to test for the role of habitat structure in affecting lethal and behavioral (non-lethal) prey-predator interactions. We used 1) the small-bodied wrasse *Symphodus ocellatus* as model prey and 2) separately, two model predators characterized by distinct foraging strategies: the stalk-and-attack *Serranus cabrilla* (hereafter 'comber') and the sit-and-wait *Scorpaena porcus* (hereafter 'scorpionfish'). These two species are among the most important predators of small-bodied fish, despite they are opportunistic macrocarnivores feeding also on crustaceans (Stergiou & Karpouzi 2002). More specifically, we tested for (i) the effects of habitat structure on prey survival/predator foraging efficiency, (ii) the effects of prey-predator co-occurrence on their habitat selection, and (iii) we comparatively described within-habitat prey-predator behavioral interactions (in terms of vertical position, activity level and prey-predator distance).

2 Materiel and Methods

2.1 Ethics Statement

All experimental work was carried out at the aquarium facilities of the zoo 'Parc Phoenix' (Nice Municipality, France). The director of the zoo's veterinary department (Dr. Pierre Escoubet), took care that the protocol adhered to the Directive 2010/63/EU of the European Parliament and of the Council, on the protection of animals used for scientific purposes. The model fish species were not available from aquaculture, so we had to collect fish individuals in the nature. The experimental fishing protocol was approved by 'Direction interrégionnale de la mer Méditerranée' (the French administration in charge of the Maritime affairs) by the permit n° 176 (released on 2011 April 18th). The sampling activity did not involve endangered or protected species and no collection within any marine protected area was performed. After collection all efforts were made to minimize damage to fish individuals. All predator individuals, and prey that had not been eaten by predators, were released alive at the end of the experiments. Fish individuals were collected between 18 April and 1 July 2011. Tank experiments were conducted during 2 May - 15 July 2011 period.

2.2 Fish collection and housing

All the individuals used for the tank experiments were collected by scuba diving in shallow rocky reefs at Villefranche-sur-Mer Bay, French Riviera (43° 41′ 42.77″ N, 7° 18′ 28.10″ E). Fish individuals were first selected by eye in order to have fish sized as homogeneous as possible, and then they have been measured (TL) to the nearest mm. Wrasses [mean TL (SD): 46 (2.7) mm; n = 60] and scorpionfish [138 (9.6) mm; n = 32] were caught using hand nets, while combers [130 (4.6) mm; n = 44] were fished using lines and hooks.

After collection, fish were held separately by species in tanks. Holding tanks (capacity between 340 and 620 l) and experimental tanks (see below) were filled with synthetic sea water (salinity: 37 (+/- 0.5) p.p.m.; temperature nearly constant at 21°C; 16h/day of artificial neon light) oxygenated with a water pump and filtered through polyamide membrane. Physicochemical parameters pH, KH, Ca, NO2 and NO3 were checked using 5 in 1 test strips, and water was renewed when necessary. Fish were fed every days: wrasses with defrosted brine shrimp *Artemia salina* and predators with defrosted mussels *Mytilus galloprovincialis*. Before using fish individuals for the experiments, they were hosted from 14 to 30 days in holding tanks, until their recovery and acclimation to tanks and artificial algae (D'Anna *et al.* 2012). Fish were not fed for 24h before the experiment started, to be sure they started from the same starvation status.

2.3 Experimental design and procedures

We used as experimental tanks four identical tanks 100 x 60 x 40 cm. Experimental tanks were placed without vis-à-vis, within the same room than holding tanks and had the same water treatment, plus an activated-carbon filter, which was added for removing dissolved fish chemical cues from trial to trial (Martin *et al.* 2010). Water pumps were stopped during data collection for excluding noise and stream disturbances.

We created 4 distinct types of artificial habitats: barren (B), shrub(S) and forest(F), plus a choice arena (CA). This latter was specifically dedicated to test a putative habitat preference for forest over shrub. It was composed by 50% shrub and 50% forest (Figure 1). The bottom of each habitat was covered with a green carpet of velour. In the other two habitats than the barren, green plastic algae were added to the carpet, one every 10 cm (100 indiv. m^{-2}). Each artificial algae (model P13EL of PENN-PLAX as raw material; (Cheminée *et al.* 2013)) was made with five stems 5 cm long for shrub, and five stems 15 cm long for forest. Before every trials, we randomly set-up the 4 distinct habitats within the 4 experimental tanks. The choice arena was randomly oriented within its tank (*i.e.* forest on the left or the right).

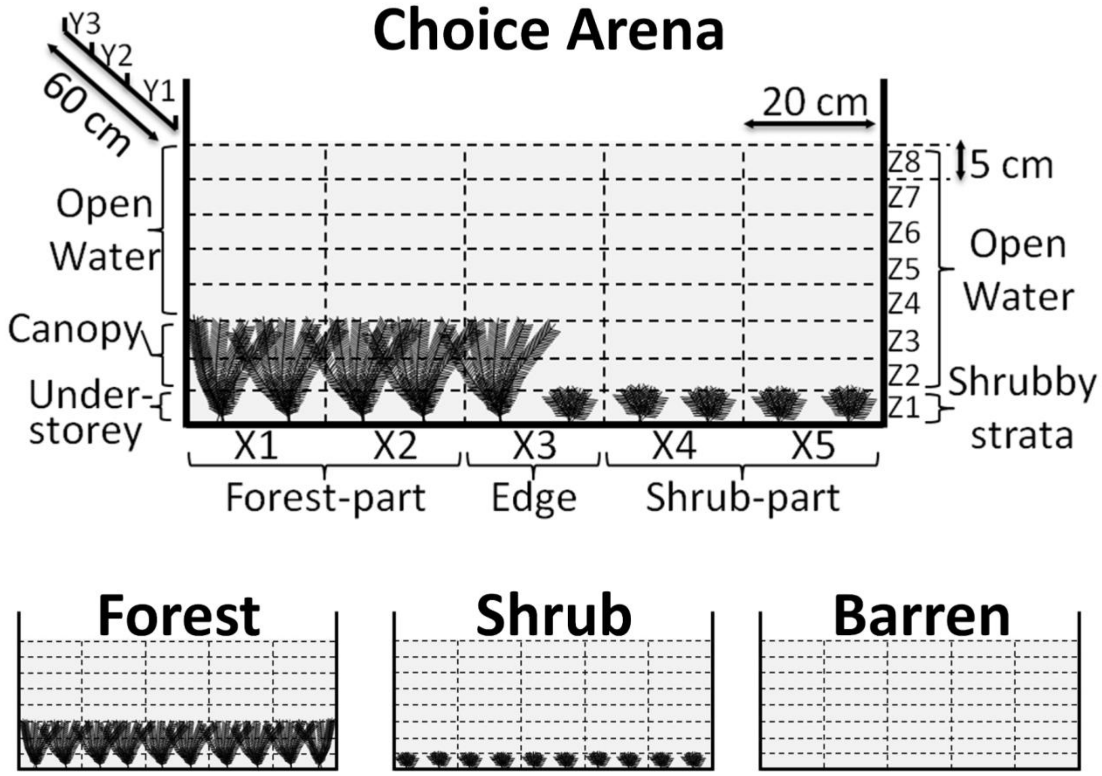

Figure 1. Schematic representation of the 3 artificial habitat-types and the choice arena. Tanks were 100 x 60 x 40 cm and virtually divided by a 3D grid (X, Y and Z axis) for recording fish positions. Stems of plastic algae were used for mimicking vegetation.

Crossed to habitat treatments, we performed 5 distinct prey-predator treatments. Three treatments involved one individual alone and were used as controls (see statistical analyses section): they included one wrasse (W), one scorpionfish (S), and one comber (C). The two other prey-predator treatments involved one prey and one predator together: one scorpionfish and one wrasse (WS), and one comber and one wrasse (WC). Prey and/or predator were introduced within the experimental tank one hour before starting data collection. This enabled fish to de-stress from manipulation, and visit and accustom to experimental tank. For treatments including both prey and predator, individuals were isolated from each other during the 1H accustoming period by an opaque plastic plank. Hence, within the choice arena, both prey and predator had access to the two habitats. Trials started as soon as the opaque separation planks were removed.

Every combination of habitat and prey-predator treatments was replicated 4 times (*i.e.* 4 trials), excluding the combinations involving the prey-predator treatment WC, which were replicated 7 times. Higher replication for WC was due to the short survival time of prey when exposed to comber (see results), and aimed at collecting enough behavioral data. Every single fish individual was used for only one trial, to avoid any possible dependence between replicates.

2.4 Survival and behavioral data collection

All observations were diurnal (artificial light). It was not possible to observe and/or record encounter, attack and capture rates, because wrasse individuals in the forest were not permanently visible. In 3 preliminary trials, wrasse never stayed unseen longer than 30 sec. Consequently, we used a multiple snapshot sampling strategy, by recording survival and behavioral data of prey and/or predator on 63 occasions during each trial. Each trial lasted 130 min, and data were collected on 21 occasions (every 30 seconds) per each of 3 observational sessions 10 min long - S1: from 0 to 10 min; S2: from 60 to 70 min; S3: from 120 to 130 min. For WC treatments, predation events interrupted observations, thus the total number of behavioral observations per trial were lower than the 63 possible occasions per trial. For WS treatments, prey survived to the 130 min trials, so we kept getting data on survival until prey disappeared due to predation.

Positions were recorded using semi-quantitative variables. Tanks were virtually divided into a 3D grid. The horizontal axes X and Y were split every 20 cm and the vertical axis Z was split every 5 cm. It is worth noting that Z values do not match the same micro-habitats depending on the habitat type (Figure 1). For getting an estimate of prey-predator distance, we transformed categorical positions into numerical coordinates (by taking the middle of the intervals) and used Euclidean distances.

Predator activity was recorded using two categories: mobile *vs* motionless (Savino & Stein 1989). Prey activity was recorded using three categories: mobile, exposed motionless, hidden motionless. This latter category was used when the prey pasted its body against a stem of algae.

2.5 Statistical analysis

2.5.1 Effects of habitat structure on lethal interactions

Prey survival (or predator foraging efficiency, depending on the perspective) was analyzed separately for the two predators due to the different number of replicates and because time scales were distinct (hours *vs* days, see results). To compare between habitats of the percentage of prey alive over time (*i.e.* prey survival curves), we fitted the class of non-parametric maximum likelihood estimators of the survival functions. This enabled to properly deal with the non-uniqueness of survival functions inherent in the interval-censoring nature of our data (see details in Fay & Shaw 2010). We tested for equality of survival functions between habitats by using Asymptotic Log-rank (Sun's scores) k-sample test. When equality hypothesis was rejected, we performed pair-wise comparisons between pairs of habitats by using asymptotic log-rank 2-sample test on data subsets and Holm-corrected p-values. All the survival analyses were implemented with the 'interval' package (Fay & Shaw 2010) for the R statistical and programming environment (R Development Core Team 2013).

2.5.2 Statistical unit and general method used for comparing averaged behavior between habitats

When comparing prey or predator behaviors between habitats and prey-predator treatments, we aggregated behavioral observations at the individual level in order to get independent statistical units. For getting a representative average behavior, we kept trials that included at least 21 observations (*i.e.* trials with the prey alive after the first observational session ended). This excluded all WC trials within barren, 1 WC trial within shrub and 1 within forest (see 'Survival results'). All univariate and multivariate permutational analyses of variance (PERMANOVA) and subsequent pair-wise tests were conducted with the software PRIMER 6/ PERMANOVA+, using Euclidean distance and 9999 permutations under the reduced model. Marginal sums of square (type III) were used since designs were unbalanced and some cells were empty. Monte-Carlo p-values were considered when not enough permutations were possible (*i.e.* < 200, Anderson *et al.* 2008). We also estimated 95% confidence intervals of all reported mean values, using 9999 bootstrap re-sampling of fish individuals.

2.5.3 Effects of prey-predator co-occurrence on their respective habitat selection

Habitat selection (choice between forest and shrub) was investigated for each species under each prey-predator treatment (the species alone or with prey/predator). The Jacob's D Selection Index (SI, Jacobs 1974) was compared between the choice arena (half forest, half shrub, see Figure 1) and the two homogenous habitats (Forest and Shrub), which served as controls for the artifact. Indeed, in control habitats, selection for a particular side of the tank, despite both sides are identical, might indicate artifact. SI was computed for each individual fish (the independent sampling unit) as follow:

$SI = \frac{n_S - n_F}{n_S + n_F}$, where the n were the number of time the individual was observed in the forest-part (n_F, *i.e.* X1 and X2 pooled) and shrub-part (n_S, *i.e.* X4 and X5 pooled) of the choice arena (Figure 1). In the two control habitats shrub and forest, n_F and n_S matched the orientation of the respective parts of the choice arena (that was randomly oriented prior every trial). Edge part (X3) was excluded for not confounding habitat selection with possible edge effect.

SI ranges between -1 and 1. $SI_{choice\text{-}arena}$ = -1 means perfect selection of forest-part over shrub-part in the choice arena. $SI_{shrub\ or\ forest}$ = -1 means perfect selection of the part of the control tank that was oriented in the same direction than the forest-part of the choice-arena. SI = 1 means the opposite. SI = 0 means no selection. Hence, we considered that habitat selection holds if in average $SI_{shrub} = SI_{forest} = 0 \neq SI_{choice\text{-}arena}$. For each species, we tested for putative differences in mean SIs between habitats (S, F, CA) and prey-predator treatments (alone or with prey/predator) using 2 ways crossed (univariate) permutational analysis of variance (PERMANOVA) and then performed pairwise comparisons whenever necessary. We assessed signs (< 0, = 0 or > 0) of mean SI values using their 95% confidence intervals.

2.5.4 Effects of habitat structure on averaged behavioral interactions

Fish individual's average behavior (in terms of vertical position, activity level and prey-predator distance) were compared between habitats and prey-predator treatments. Distributions of vertical position (Z) and Prey-Predator distance (PPD) consisted in 21 to 63 semi-quantitative measures per individual fish. In order to aggregate distributions at the level of individual fish (the independent sampling units), we used the mean and the standard deviation of each individual fish’s distribution. The standard deviation (hereafter referred to "variation") may be seen as a proxy of the preference strength for the mean value. We thus obtained four aggregated variables: mean vertical position, vertical variation (around the mean), mean PPD and PPD variation. Mean of each variable was compared between habitats (B, S, F) and prey-predator treatments using univariate PERMANOVA. The categorical variable 'activity' was expressed for each individual fish as frequencies per category. Frequencies were organized in a matrix (fish individual X category) and were compared between habitats and prey-predator treatments using multivariate PERMANOVA.

3 Results

3.1 Effects of habitat structure on lethal interactions

As a general rule, predators' foraging success were reduced by increasing habitat complexity. Wrasse survival curves, in fact, were significantly different between habitats when wrasses were exposed to scorpionfish (Log-rank test, $X^2 = 11.8$, df = 3, *p*-value=0.008) and comber (Log-rank test, $X^2 = 40.3$, df = 3, *p*-value < 0.001). In both cases, survival curves were sharper in barren than in forest and choice arenas (half shrub - half forest), and intermediate in shrub (Figure 2). Despite prey survival curves were not statistically compared between predators, combers preyed faster upon wrasses than scorpionfishes. All predation events occurred within 130 minutes in the arenas with comber, while predation events occurred only from the second-third-day interval in the arenas including scorpionfishes. For the 7 replicates of the wrasse-comber treatment, wrasses were preyed before the first observational session ends (*i.e.* < 10 min, Figure 2). Hence, subsequent analyses on positions and behavior were not possible for this treatment.

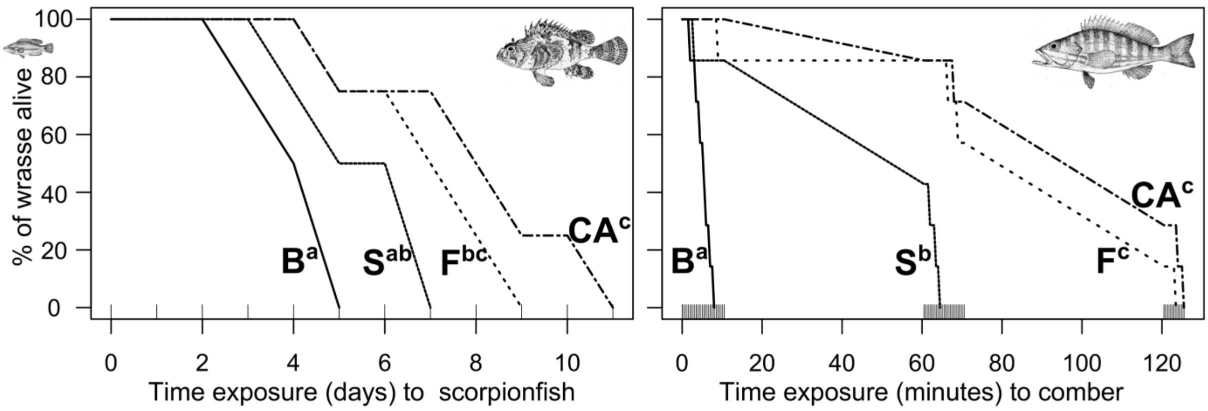

Figure 2. Survival curves of wrasses depending on habitat-types and predator identity. Wrasses were exposed to scorpionfish (left) and to comber (right) in the habitats of increasing complexity: Barren (B), Shrub (S) and Forest (F), and in the Choice-Arena (CA). In each graph, curves sharing a lower case letter were not significantly different. Upper tick marks on the axis X delimit the censored intervals.

3.2 Effects of prey-predator co-occurrence on their respective habitat selection

Wrasse habitat selection was related to the presence and identity of the predator (Table 1). Wrasses preferred the forest over the shrub when they were alone or in the presence of comber, while no habitat selection was observed in the presence of scorpionfish. More specifically, for both treatments W and WC, pair-wise comparisons of SIs (Figure 3) revealed that mean SIs differed between controls and choice arena, being close to 0 in controls and negative in choice arena (*i.e.* mean SI_{shrub} = mean SI_{forest} = 0 > mean $SI_{choice\ arena}$). Moreover, mean $SI_{choice\ arena}$ was more negative for W than for WC treatment. This may indicate that the presence of comber strengthen wrasses' preference for forest. On the contrary, when wrasses were in the presence of scorpionfish, they did not select any habitat since mean SIs did not differ between habitats and were close to 0.

Scorpionfish habitat selection was not clearly highlighted by our tank experiment. Despite scorpionfish in choice arena spent most of the time in the forest-part (mean SIs ≤ 0 according to 95%CI, Figure 3), we cannot draw any conclusion about habitat preference. In the forest habitat, scorpionfish (with wrasse, WS) spent most of the time within the same side of the tank compared to the side of the forest-part of the Choice Arena (mean SIs ≤ 0 according to 95% CI, Figure 3), while forest habitat was homogenous and no preference was therefore expected (control habitat, see M&M).

Combers habitat selection was independent upon the wrasse absence/presence (Table 1). Combers preferred the forest over the shrub. More specifically, combers' SIs were significantly different between habitats and pair-wise comparisons (Figure 3) revealed that mean SIs differed between controls and choice arena (*i.e.* S = F ≠ CA), being close to 0 in controls (confidence intervals including 0) and negative in choice arena.

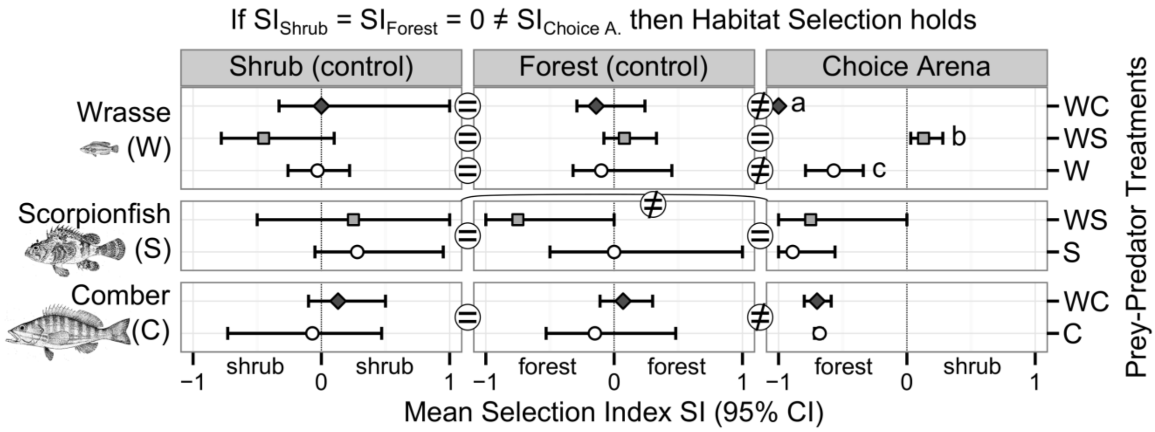

Figure 3. Habitat selection of prey and predators depending on prey-predator treatments. Selection Index (SI) mean values (95% CI) in controls (shrub and forest) and choice arena. In choice arena, SI < 0 means selection of forest-part over shrub-part, SI > 0 means the opposite. Results of post-hoc pair-wise comparisons are reported using equal/unequal symbols or lower case letters. See Material and Methods for more details.

Table 1. PERMANOVA on Selection Index. Pr: Prey-Predator Treatments; Ha: Habitat. ns not significant; ° p < 0.1; * p < 0.05; *** p < 0.001

	Wrasse				Scorpionfish				Comber			
Source	df	SS	F		df	SS	F		df	SS	F	
Pr	2	0.68	1.38	ns	1	0.28	0.5	ns	1	0.13	0.86	ns
Ha	2	1.36	2.75	°	2	4.77	**4.32**	*	2	3.18	**10.25**	***
PrxHa	4	3.17	**3.21**	*	2	0.89	0.81	ns	2	0.09	0.30	ns
Res	34	8.40			18	9.94			25	3.87		
Total	42	14.65			23	15.87			30	7.72		

3.3 Effects of habitat structure on averaged behavioral interactions

3.3.1 Activities

Wrasses' activities were different between prey-predator treatments (Table 2). When alone and in the presence of scorpionfish, wrasses were mobile during 81% (77, 84) of the observations (mean (95 % CI)) and were exposed motionless during all the other observations. Contrastingly, in the presence of comber, wrasses were observed (only in Shrub and Forest, see M&M) to move actively at 21% (17, 26), exposed motionless at 4% (2, 6), and hidden motionless at 75% (71, 79).

Scorpionfish were observed motionless most of the time, but some slight differences were detected (Table 2) between the absence (97% (90, 99)) and the presence of wrasses (100% (98, 100)), and between habitats: motionless at 94% (88, 98) in barren, at 99% (94, 100) in shrub, and at 100% (99, 100) in forest.

Combers' activities were dependent on the presence of wrasses (Table 2). Combers were observed as many times mobile (52% (50, 55)) and motionless (48% (43, 51)) when they were alone, while comber's mobility increased to 71 % (69, 76) when they were in the presence of a wrasse.

Table 2. PERMANOVA on proportions per activity categories. Pr: Prey-Predator Treatments; Ha: Habitat. ^{ns} not significant; ° $p < 0.1$; * $p < 0.05$; *** $p < 0.001$

	Wrasse				Scorpionfish				Comber			
Source	df	SS	F		df	SS	F		df	SS	F	
Pr	2	6.03	**129.74**	***	1	0.02	**4.66**	*	1	0.34	**111.23**	***
Ha	2	0.05	1.13	ns	2	0.03	**3.96**	*	2	0.01	1.26	ns
PrxHa	3	0.03	0.37	ns	2	0.02	2.67	ns	1	0.00	0.01	ns
Res	28	0.65			18	0.06			19	0.06		
Total	35	7.87			23	0.12			23	0.47		
	Pr: W = WS ≠ WC				Ha: B = S ; S=F ; B ≠ F							

3.3.2 Vertical distribution

Wrasses adapted their vertical distribution in response to the interaction of habitat and prey-predator treatments (Table 3 and Figure 4A), with major changes (relatively to wrasses alone) taking place in responses to scorpionfish's presence and minor changes in responses to comber's presence.

Wrasses in the absence of predators adapted their vertical distribution in response to the vegetation height (Figure 4A and Table 3). In barren, devoid of vegetation, wrasses did not prefer any specific vertical stratum. Indeed, mean positions equaled 15 cm (around the middle of the water column) and position variations were high (Figure 4A). On the contrary, in the vegetated habitats, vegetated strata were preferred. Position variations were lower, involving an increased preference for mean positions, which were also lower. Mean positions were higher in forest than in shrub (Figure 4A), but the greater vegetation height in forest compared to shrub enabled wrasses to occupy more frequently the vegetated strata in forest than in shrub: in forest, 92% (88,96) of the observations (mean (95% CI)) within vegetated strata (understory and canopy); in shrub, 79% (65,90) of the observations within shrubby stratum

(Figure 4B). Nevertheless, in both vegetated habitats, wrasses in the absence of predators clearly preferred the vegetated strata over open water.

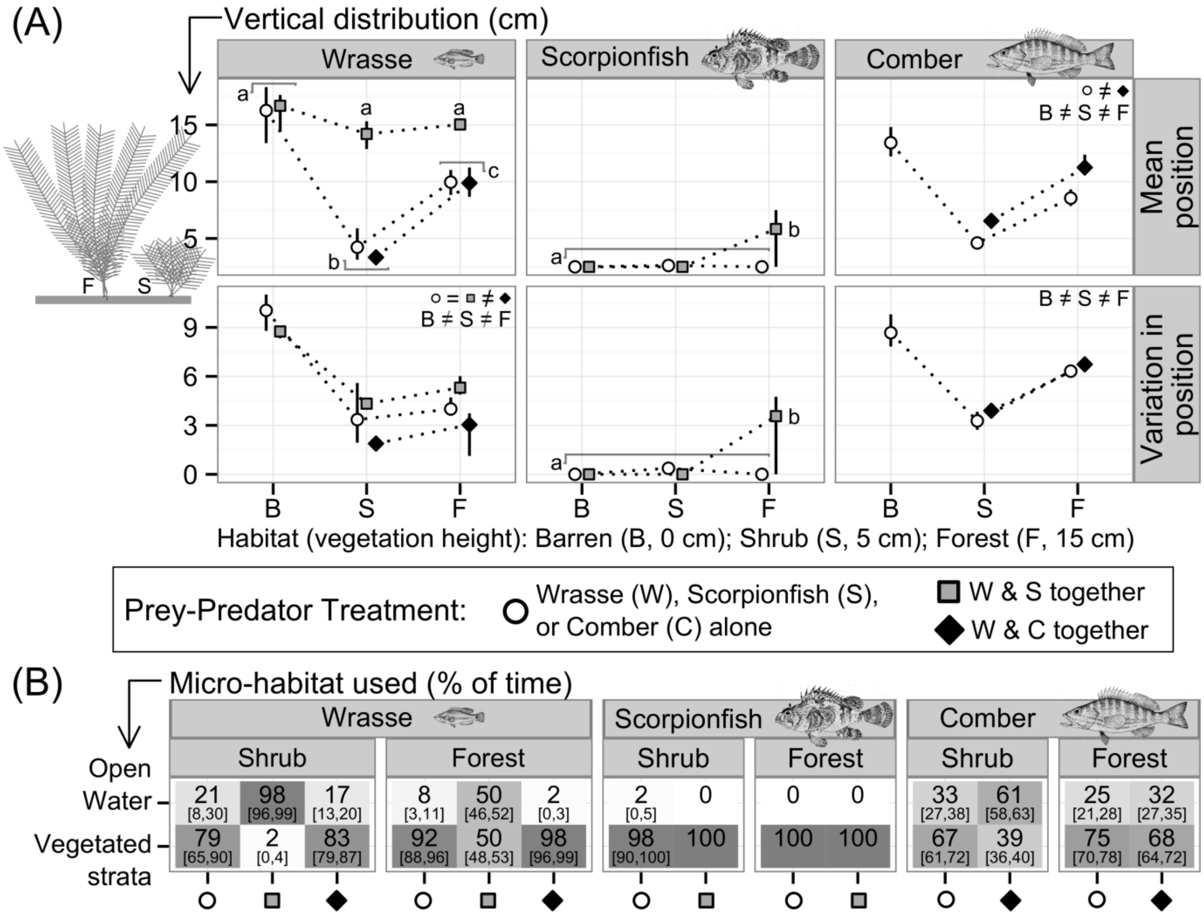

Figure 4. Vertical distributions of prey and predators depending on vegetation height and prey-predator treatments. (A) values averaged over replicates [95% CI] of the means (Mean position) and the SDs (Variation in position) of every individual's vertical distributions. Results pair-wise comparisons post-hoc to ANOVA (Table 3) are reported using equal/unequal symbols or lower case letters. (B) Mean frequencies [95% CI] of the time spent within the vegetated strata (0 to 5 cm in Shrub, 0 to 15 cm in Forest) and within open-water.

Wrasses deeply changed their vertical distribution when they were exposed to scorpionfish in shrub and in forest. Preference for vegetated strata was replaced by preference for intermediate distance from the bottom, independently of the habitat. Indeed, mean positions were in both habitats around 15 cm up to the bottom with moderate position variations (Figure 4A) what led to distinct frequencies of vegetated strata occupation (Figure 4B). In barren, mean positions were also around 15 cm up to the bottom but position variations were higher, as for wrasses in the absence of predators (Figure 4A).

Wrasses changed slightly their vertical distributions when they were exposed to comber. Mean positions and percent of time spent within vegetated strata did not changed (Figure 4B), only position variations were reduced (Figure 4A).

Scorpionfish's vertical distributions responded significantly to the interaction between habitat and prey-predator treatments (Table 3 and Figure 4A), being all identical except for scorpionfish in forest with wrasse. Excluding this latter case, scorpionfish had almost always been observed sit on the bottom. With regard to the exception of the scorpionfish in forest in the presence of wrasse, we observed scorpionfish at 33 % (8,50) sit in the upper-most part of the canopy, and at 67% (42,83) sit on the bottom below the canopy.

Combers adapted their vertical distribution in response to habitat treatments (in terms of both mean position and position variations) and in response to prey presence (in terms of mean positions) (Table 3 and Figure 4A).

Combers alone adapted their vertical distribution in response to the vegetation height (Figure 4A and Table 3). In barren, combers did not prefer a specific vertical stratum, since mean positions equaled the middle of the water column and position variations were high (Figure 4A). On the contrary, position variations were intermediate in forest and low in shrub (Figure 4A) meaning that preference for mean positions increased in the vegetated habitats. Mean positions were higher in forest than in shrub (Figure 4A), but canopy and shrubby strata were similarly frequented. Indeed, combers alone in shrub habitat were observed at 67% (61, 72) within shrubby stratum, and combers alone in forest habitat were observed at 75% (70, 78) within vegetated strata (Figure 4B). Hence, combers in the absence of wrasse preferred vegetated strata over open water, in both vegetated habitats.

Combers adapted their vertical distribution in response to the presence of wrasse, by increasing their mean positions (Figure 4A). In shrub, this resulted in a decrease of the time spent in the shrubby strata (39% (36, 40)). In forest, the time spent within the whole vegetated strata did not significantly decrease (68% (64, 72), Figure 4B).

3.3.3 Prey-Predator Distances

Distributions of prey-predator distance (PPdist) were different between habitat treatments in terms of mean (2 ways PERMANOVA, only term Ha significant: Pseudo-$F_{3,28} = 13.37$, $p < 0.001$), and were different between prey-predator treatments in terms of variation (2 ways PERMANOVA, only term Pr significant: Pseudo-$F_{1,28} = 15.76$, $p < 0.001$). Post-hoc tests (Figure S1) revealed that Mean PPdist were greatest in barren and shrub, intermediates in forest and lowest in choice arena. PPdist Variation was higher with combers than with scorpionfish (Figure S1).

Table 3. PERMANOVA on mean and variation of fish individual's vertical distribution. Pr: Prey-Predator Treatments; Ha: Habitat Treatments. Pr: Prey-Predator Treatments; Ha: Habitat. ^{ns} not significant; ° $p < 0.1$; * $p < 0.05$; *** $p < 0.001$.

	Wrasse					Scorpionfish					Comber				
		Mean		Variation			Mean		Variation			Mean		Variation	
Source	df	SS	F	SS	F	df	SS	F	SS	F	df	SS	F	SS	F
Tr	2	283.59	**57.70** ***	22.56	**9.44** ***	1	6.89	**5.54** *	6.80	**6.59** *	1	25.87	**26.67** ***	1.29	2.90 ^{ns}
Ha	2	297.46	**60.52** ***	147.21	**61.58** ***	2	14.31	**5.75** **	15.36	**7.44** **	2	215.12	**110.91** ***	81.71	**91.98** ***
TrxHa	3	109.74	**14.89** ***	8.18	2.28 ^{ns}	2	15.37	**6.17** **	18.88	**9.14** **	1	0.68216	0.70 ^{ns}	0.05	0.11 ^{ns}
Res	28	68.81		33.47		18	22.39		18.58		19	18.43		8.44	
Total	35	960.22		288.36		23	58.95		59.61		23	241.27		94.93	

3.4 Within habitat description of short-term behavioral interactions

Beside the analysis of the effects of habitat structure on the averaged behavioral interactions reported above, we also quantitatively analyzed within-habitat short-term behavioral interactions. Methods and raw results are provided in the Supporting Information S1. In brief, Figure 5 schematically represents how prey and predator activity, vertical positioning and distance to each other interact within each habitat.

Within Barren, the wrasse in presence of the scorpionfish (Figure 5-A) moved across every strata of the water column but wrasse's movements were constrained by scorpionfish positions. When the wrasse was passing above the scorpionfish laid on the substrate, the wrasse increased its vertical distance from the substrate. Wrasse used the same tactic face to the scorpionfish within shrub and forest, with some slight variants. The wrasse was not moving close to surface nor to the substrate in both vegetated habitats (Figures 5-B and 5-C.1), excluding when the scorpionfish was laid on the canopy of the forest (Figure 5-C.2). In the latter case, the wrasse reacted by increasing its distance from the substrate. Hence, the wrasse always adapted its vertical position for avoiding immediate vicinity with the scorpionfish.

The wrasse behaved differently face to the comber. In both vegetated habitats, the wrasse remained most of the time hidden within the vegetated strata (Figures 5-D.1 and 5-E.1). Wrasse's movements differed between habitats. In shrub, the wrasse mainly moved in open-water just above the shrubby strata, and to a lesser extent within the shrubby strata (Figure 5-D.2). In forest, the wrasse always moved within the vegetated strata (Figure 5-E.2). In regard to the use of the different vegetated strata of the forest, the wrasse hided always within the canopy, and moved within the canopy and within the understory (Figure 5-E.1.2).

4 Discussion

Fishes are more abundant and diversified within structured habitats (*e.g.* Bostrom *et al.* 2006). This patterns is shared by both prey and predator fish, that often co-habit in the same habitats (Sheaves 2001). However, their behavioral interactions within structured habitats and the role of habitat structure is not well known. We analyzed how prey use the 3D habitat structure in terms of scenarios where to adopt specific anti-predator behavior patterns, within the 3 habitat-types investigated, face to two predators using distinct foraging strategies. The first conclusion of our tank experiments is that the wrasse *Symphodus ocellatus* has an adaptive anti-predator behavior related to habitat structure (in forested and, to a lesser extent, shrub) face to the stalk-and-attack predator, *i.e.* the comber *Serranus cabrilla*. Oppositely, wrasse adaptive anti-predator behavior face to the sit-and-wait scorpionfish *Scorpaena porcus* does not depend upon habitat structure. Our results suggest that habitat vertical stratification may be an important factor influencing lethal and behavioral prey-predator interactions, and consequently it may contribute to the co-existence of prey and multiple predators within structured habitats.

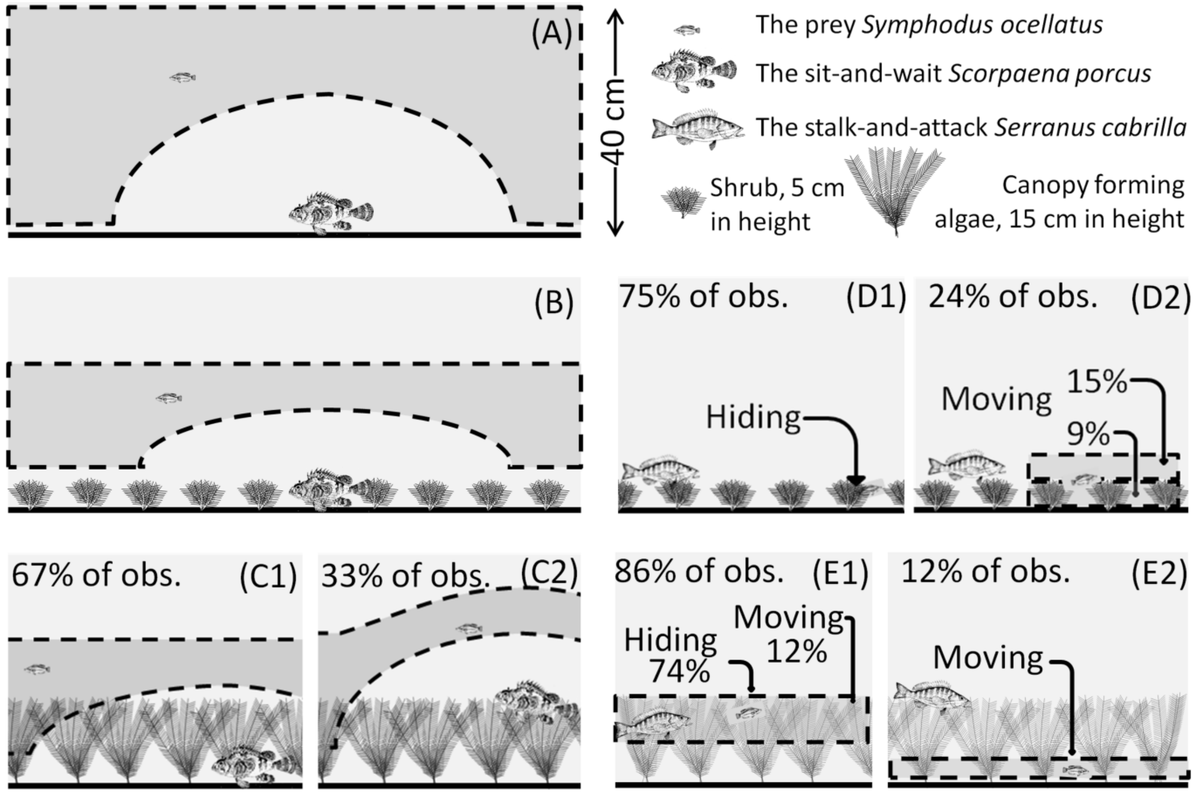

Figure 5. Schematic representations of the predator-specific anti-predator behavior of wrasses, depending on habitat types. (A to C) wrasse and scorpionfish behavioral interactions, (D and E) wrasse and comber behavioral interactions. Formal tests of associations among categories of activity, prey and predator positions and prey-predator distances are reported in Supplementary Information S1.

4.1 Habitat structure *per se* affects fish habitat selection

Artificial algae were used in our tank experiments in order to assess the putative effects of habitat structure *per se*, without any possible confusion with other factors such as food (normally associated with natural algae). With regard to the behavior patterns of the three species observed individually, wrasse and comber adapted their vertical distribution in response to vegetation height. Moreover, wrasse, comber, and scorpionfish (even though for this latter we cannot exclude a possible artifact effect) preferred the forested structure over shrubby structure. These observations suggest that habitat structure *per se* is an important factor affecting fish decision making about both vertical distribution and habitat selection. With regard to behavior patterns when prey and predator are together, predation risk (foraging opportunity, respectively) seems to be less important than habitat structure in influencing decision making of prey (predator, respectively) about habitat selection. Wrasse facing comber in the choice arena was still choosing the forest-part. This took place despite the immediate vicinity of the comber, which was choosing the forest-part too. Wrasse preference for the predator rich habitat represented by forest might be related to the fact that prey may escape predation thanks to the forest canopy (see below), which may overcome the higher encounter rates with predators (Lima 1992). Comber preference for forest, on the other hand, does not necessarily reduce its foraging efficiency in the field. Forests host higher densities of comber's favored prey (small fish and macroinvertebrates) (Stergiou & Karpouzi 2002;

Gozler *et al.* 2010). This may give comber more opportunities to attack, what may overcome the lower attack success and insure an overall better foraging success (Lannin & Hovel 2011). Wrasse facing scorpionfish did not select any part of the choice arena. This lack of selection resulted probably from two conflicting demands: wrasse preference for forested structure and the avoidance of scorpionfish, which was always sat in the forest part of the choice arena. In the field, wrasse probably may solve this conflict by moving few meters apart but still in forest (see below).

Habitat selection could be primarily due to habitat preference, *i.e.* a decision making that don't need to be triggered by predation risk or food availability, habitat structure solely is enough for attracting fish (Tait & Hovel 2012; Horinouchi *et al.* 2013). However, habitat preference may be a proactive behavior, eventually learned and/or selected through predation and/or foraging pressures (Bell & Westoby 1986; Dahlgren & Eggleston 2000; Morris 2003; Tait & Hovel 2012; Horinouchi *et al.* 2013). Experiments including all combinations of food availability, predation risk and habitat structure are required for assessing what are the most important proximate cue(s) used by fish for selecting habitat (*e.g.* Horinouchi *et al.* 2013). Nevertheless, our tank experiment suggests that habitat selection (and maybe primarily habitat preference) may induce net immigration of fish into forest and contribute to shape the density patterns observed in the field: higher fish diversity and abundances observed in *Cystoseira* forests (Orlando Bonaca & Lipej 2005; Sala *et al.* 2012; Cheminée *et al.* 2013).

4.2 Wrasse-comber within habitat behavioral interactions

We observed that comber employed an active search foraging strategy in every habitats. Comber increased its mobility in response to wrasse presence and it explored the same micro-habitat than wrasse (the respective vertical distributions of comber and wrasse matched in every habitats). This observed behavior coincides with the well-known diurnal stalk-and-attack foraging strategy of the comber (Viladiu *et al.* 1999; Alos *et al.* 2011). In response to comber presence, wrasse reduced its mobility and hide within vegetation when available (*i.e.* in shrub and forest habitat), with a clear preference for hiding in forest over shrub habitat. The absence of vegetated strata in barren did not allow wrasse to hide. This explains the lowest survival rates observed in barren. Wrasse preference for forest over shrub (habitat-choice experiment) and its highest survival in forest compared to shrub were likely due to the higher habitat complexity of forest, but maybe more specifically to its vertical stratification. In forest habitat, wrasses were using most of the time the more dense upper part of the canopy (branches and leaves) for hiding when predators were close. This was probably because high structural complexity limits visual cues for predator and/or reduces predator mobility (Main 1987; Horinouchi 2007). In less occasions, wrasses were observed to move. In forest, wrasses were moving within the canopy and also within the less dense understory (trunks), especially when comber was up to the canopy. This tactic seems to rely on the particular stratification of the forest: an understory suitable for fast prey movement, moreover well protected by the canopy above that acts as a horizontal barrier preventing predator displacements. On the contrary, in shrub habitat, wrasses were moving by passing among shrubs and also by passing above the shrubby strata. This latter tactic might be used to widen the field of view in order to better assess predation risk (McCormick & Lonnstedt 2013). Doing so, wrasses are not hidden and easier to detect by combers. We suggest that forest, compared to shrub, increase efficiency of wrasse anti-comber behavior by providing more hiding opportunities thanks to higher structural complexity (canopy *vs* shrubby strata) and/or by providing more escape/avoidance opportunities thanks to the presence of an understory below the canopy.

4.3 Wrasse-scorpionfish within habitat behavioral interactions

We observed that scorpionfish were always sited on the bottom, except in the forest in the presence of wrasse, where scorpionfish was sitting also upon the forest canopy. Wrasse's anti-scorpionfish behavior consisted in avoidance and this did not depend on the habitat structure, at least during our diurnal observations. Indeed, wrasse did not select any of the two habitats during our habitat-choice experiment, and on the other hand wrasse behaved similarly within each habitat. Within each habitat, wrasse was moving and increased its vertical position when passing above the predator, in order to avoid its immediate vicinity. This avoidance tactic was efficient since wrasses survived at least 3 days. This efficiency is likely due to scorpionfish sit-and-wait strategy that can succeed only if the prey enters its small attack range (Huey & Pianka 1981). In the field where fish are not confined, the avoidance tactic we observed probably leads wrasse to move few meters apart from the sit-and-wait predator. From this perspective, increasing vertical distance from the predator (hereafter referred as 'vertical avoidance') may be the initial response to predator detection, followed by an horizontal avoidance (within or across habitats). Horizontal avoidance of sit-and-wait predator is well known, especially in the context of habitat-selection. Numerous study in freshwater (*e.g.* Eklov & Persson 1996; Martin *et al.* 2010) and marine systems (Horinouchi *et al.* 2009; Smith *et al.* 2011) reported such behavior where prey avoid a sit-and-wait predator laid in the vegetated habitat by shifting to the adjacent predator-free non-vegetated habitat. Contrastingly, the only example of vertical avoidance we found in the literature concerning bentho-pelagic systems is the y-0 cod (*Gadus moruha*) facing the sit-and-wait sculpin *Myoxocephalus scorpinus* (Laurel & Brown 2006). Early vertical avoidance of wrasse face to sit-and-wait predators within stratified habitats may be related to the fact that detection of predators hidden within the complex stratum may be olfactive before being visual (Martin *et al.* 2010). A prey that detects olfactively the presence of a sit-and-wait predator but that did not exactly locate it (visually), may have advantage to, as soon as possible, avoid the dangerous complex stratum by directly going up into the open-water strata.

4.4 The apparent low foraging efficiency of scorpionfish

Scorpionfish needed at least 3 days (and nights) for capturing wrasse. This apparent low foraging efficiency may be due to several possible explanations. (1) Scorpionfish may have been un-hungry during first days, thanks to the low energy cost of sit-and-wait strategy (Huey & Pianka 1981) and/or due to post-manipulation stress (transfer from holding to experimental tank). Or, (2) scorpionfish might have wait during first days, expecting simply we feed them with mussel (conditioned to tank), or more naturally expecting other prey easier to catch such as brachyurans (Harmelin-Vivien *et al.* 1989). Finally, (3) scorpionfish might have tried but failed to capture wrasse during first days and nights. Considering that some stomach contents analyses revealed that scorpionfish is able to capture bentho-pelagic fish in great quantity such as the red mullet *Mullus Barbatus* (Bascinar & Saglam 2009) and even pelagic fish such as the european anchovy *Engraulis encrasicolus* (Demirhan & Can 2009), the apparent low foraging efficiency might be due to wrasse's anti-scorpionfish behavior that have been particularly efficient, at least during first days and nights. We already discussed above the efficient diurnal anti-predator behavior we observed in our experiment. In regard to the un-observed wrasse activity during the nights, they were probably resting, since the species is known to be diurnal (Harmelin 1987). Oppositely, scorpionfish have higher nocturnal activities (Harmelin-Vivien *et al.* 1989). Hence, simply the temporal mismatch between activities of the nocturnal predator and the diurnal prey may explain a low encounter rate and consequently a low predation rate (McCauley *et al.* 2012). From this perspective, scorpionfish effects on wrasses could be mostly behavioral, rather than lethal (Preisser *et al.* 2005).

Nevertheless, after some days, scorpionfish preyed on wrasses more efficiently in barren than in forest. This was unexpected because sit-and-wait foraging strategy is recognized to be not affected by structural complexity (*e.g.* Schultz & Kruschel 2010). Other studies even suggest that habitat complexity promote its efficiency (*e.g.* Horinouchi *et al.* 2009), possibly by promoting predator camouflage (Rilov *et al.* 2007) while not interfering with attack maneuver that involves only low predator displacement (small attack range). A possible explanation therefore is a shift in foraging tactic. After some days of starvation, scorpionfish may have started to actively search for prey (Savino & Stein 1989), and consequently prey could have benefited from hiding/escape possibilities offered by habitat structure in shrub and (even more) in forest, as against comber.

4.5 Vertical movements in structured habitats face to multiple predators

In the field, where wrasse co-exist with multiple predators, the wrasse anti-predator behavior face to scorpionfish (*i.e.* increased occupancy of the open water strata) is likely to increase wrasse predation risk from comber, other stalk-and-attack predators (*e.g. Serranus scriba*) and transient roving predators (*e.g. Dentex dentex*). On the contrary, wrasse anti-predator face to active searchers, (*i.e.* seeking shelter within the vegetated strata), increases predation risk face to sit-and-wait predators ambushing below the canopy. We could not test for putative interactive effects of multiple predators (Martin *et al.* 2010). In our tank experiments, we did not exposed wrasse to both predator simultaneously since this would not give reliable results as regards the size of our experimental tanks. Nevertheless, our results suggests that vertical stratification of forest allow prey fish to adapt its anti-predator behavior very quickly, by switching vertical strata, *i.e.* seeking vegetated strata versus avoiding it, depending on the strategy of the predator. From this perspective, the interface canopy/open-water in forest could be seen as an ecotone where edge effects consists in vertical movements, similarly to the ecotone between structured and unstructured habitats, where edge effects consist in horizontal movements (Smith *et al.* 2011). The adaptive shift of vertical strata involves only short-distance movements, and may allow wrasses to reduce their flight initial distance (Dill 1990). The lowest prey-predator distance we observed in forest may support this hypothesis. Flight is costly in terms of both energy and loss of foraging opportunities. Immediate vicinity of both vegetated and open-water strata in forest may therefore have also positive side-effects on wrasse energy budget.

Despite such 3D movements related to anti-predator behaviors have been scarcely documented, we believe they are common for many animals living in structured habitats. For instance, Makin et al (2010) studied anti-predator behaviors of vervet monkeys (*Chlorocebus* *aethiops*), an african primate spending, in savanna, an equal amount of time on the ground and in trees. The study highlighted an adaptive anti-predator behavior against multiple predators: when threatened by terrestrial predators (*e.g.* the leopard *Panthera pardus*) vervet monkeys can reduce predation risk by moving upwards into trees, while when threatened by aerial predators (*e.g.* eagles), they move down.

4.6 Limits inherent to tank experiments and perspectives

Our survival analysis highlighted that wrasses facing a single predator (comber or scorpionfish) use anti-predator tactics that are more efficient in forest and our behavioral observations enabled to better understand how vertical stratification of habitat benefits anti-predation tactics. Results of our survival analysis do not necessarily imply that in the field, predation mortality is the lowest in forest. Predation mortality of a given prey species is affected by (among others factors) foraging efficiency of each predator individuals, densities of predators, and also by densities of other prey species that may release the predation pressure (but that may be apparent competitors). In regard to the complexity of food web in coastal habitats, involving numerous generalist predators preying on numerous prey species, it has to be considered that only field-based experiments (where every factors may interacts) may be appropriate for comparing overall mortality rates between habitats. Experimental methods, therefore, must be chosen cautiously, by considering the habitat-specific anti-predator behaviors we presently reported. For instance, tethering experiments (predation rate assessment by tying off prey) is likely to interact with vegetation height and induce habitat-specific artifacts (Peterson & Black 1994).

Our study highlighted that habitat structure of *Cystoseira* forest may mediate lethal and behavioral prey-predator interactions and consequently may contributes to the co-existence of prey and multiple predators in higher densities in forest compared to less structured habitat. This evidence stresses the paramount role of this habitat for coastal fish assemblages (Orlando Bonaca & Lipej 2005; Sala *et al.* 2012; Cheminée *et al.* 2013) and emphasizes the need to develop better management practices of the human activities impacting *Cystoseira* sp. (Gianni *et al.* 2013). Meanwhile, some further field based experiments should be specifically designed for estimating the relative contribution of habitat-specific mortality versus habitat preference in shaping fish assemblages structure. Filling these gaps of knowledge would help predict fish assemblage structures under scenarios of greater human-driven losses of *Cystoseira* forests, when habitat choice would not be possible anymore.

Supplementary Information available at the end of the chapter:

- Figure S1. Prey-Predator distances depending on habitat-types and prey-predator treatments.
- Supplementary information S1. Method used for analyzing within-habitat short-term behavioral interactions and raw results.

Acknowledgment

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6 Supplementary Information

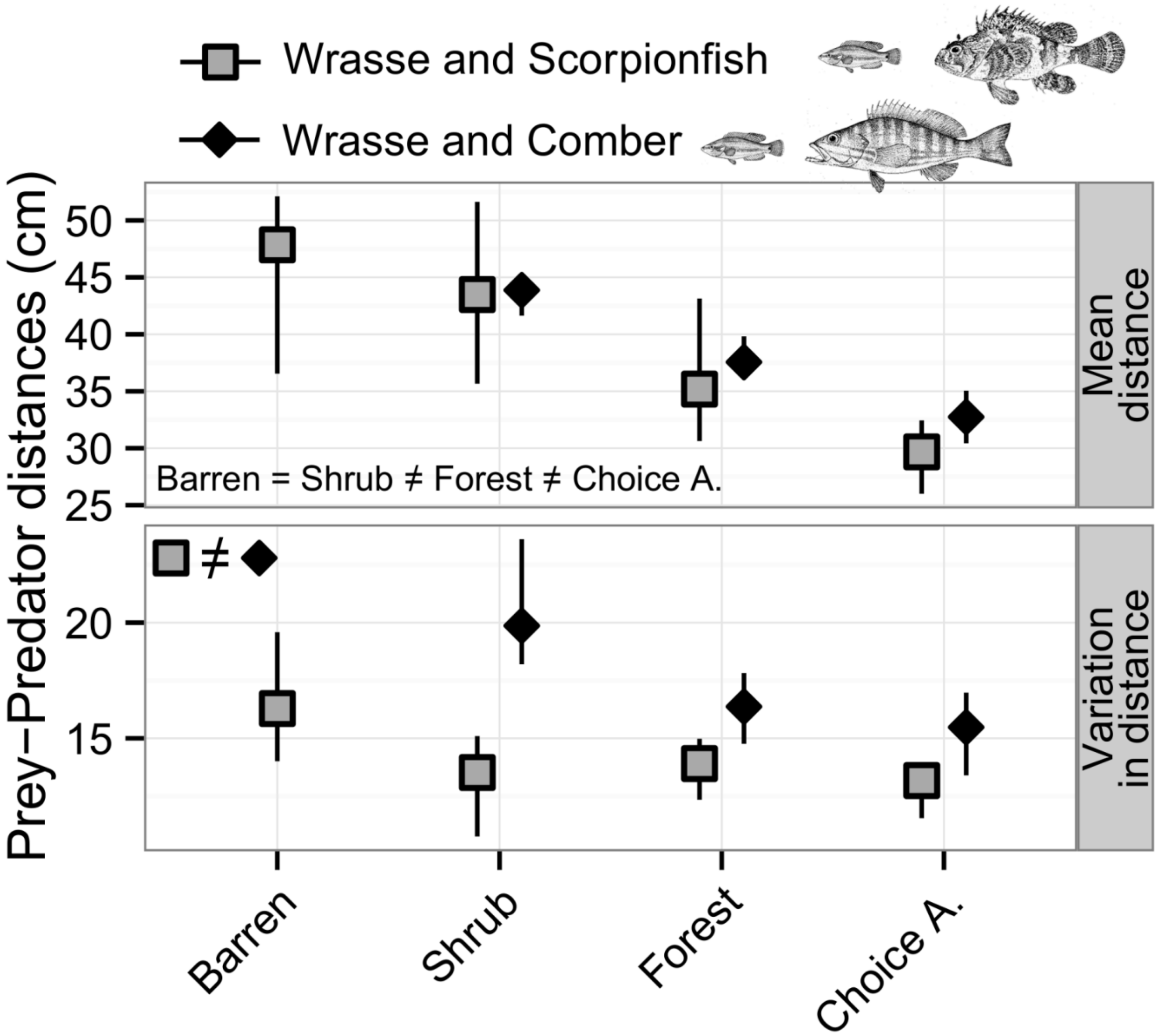


Figure S1. Prey-Predator distances depending on habitat-types and prey-predator treatments. Values averaged over replicates (95% CI) of the means (Mean distance) and the SDs (Variation in distance) of prey-predator distances' distributions. Post-hoc to ANOVA, pair-wise comparisons results are reported using equal/unequal signs.

6.1 Supplementary Information S1: Within habitat description of short-term behavioral interactions

6.1.1 Statistical analyses

Within habitat short-term prey-predator behavioral interactions were reconstructed from the multiple snapshot sampling by detecting tendencies between prey and predator respective positioning and activity, and their relative distance. Separately for each combination of habitat (S, B, F) and prey-predator treatments (WS and WC), we carried out the 3 steps Husson *et al.* (2010) method implemented in the R package 'FactoMineR' (Lê *et al.* 2008). This enabled to identify and characterize clusters of multivariate observations, which were interpretable as distinct phases of the short-term prey-predator behavioral interactions. First, we performed Multiple Correspondence Analysis (MCAs). Statistical units here were every single observational time, which were sampled every 30 sec within 3 sessions. The 5 categorical variables considered were: prey's Z position, predator's Z position, prey's activity, predator's activity, and PPD intervals. PPD was a continuous variable, so for enabling possible non-linear relationships, we cut PPD into 3 or 4 balanced intervals depending on PPD distribution. For the categorical variables, we pooled case by case, some categories for balancing distributions since MCA is sensitive to unbalance. Second, we performed a partitioning of the observations' coordinates on the principal components (PCs) using the HCPC routine (mixing hierarchical classification and K-means algorithms). We retained all the PCs needed for reaching 85% of cumulated explained variance (5 to 8 PCs) in order to stabilize the clustering by deleting the noise from the data (Husson *et al.* 2010). The optimal number of clusters was assessed by selecting the partition (among 2 to 10 clusters) having the higher relative loss of inertia (Husson *et al.* 2010). Third, we identified which categories were characterizing the clusters by using the catdes routine, which computes and assesses significance (threshold used: 0.05) of the value-test (Lê *et al.* 2008). A significantly negative value-test for a given category in a given cluster means that this category is under-represented in this cluster. A significant positive value-test means over-representation. Hence, each cluster was characterized (positively or negatively) by some categories. This was interpretable as distinct phases of the short-term prey-predator interactions. The factor Trial (each couple of prey-predator individuals) was added as supplementary categorical variable in order to detect behavioral profiles representative of every trials from individual-specific behavioral profiles (the clusters that were characterized by some particular trial(s)).

6.1.2 Results

For every combinations of prey-predator and habitat treatments, several behavioral profiles (*i.e.* clusters in MCA) were detected (Figure S2). None or few behavioral profiles were characterized by individual prey-predator couples (*i.e.* trial), suggesting that most of the behavioral profiles were not individual-specific but representative of the species interactions. We thus reported below only behavioral profiles that were not characterized by a trial.

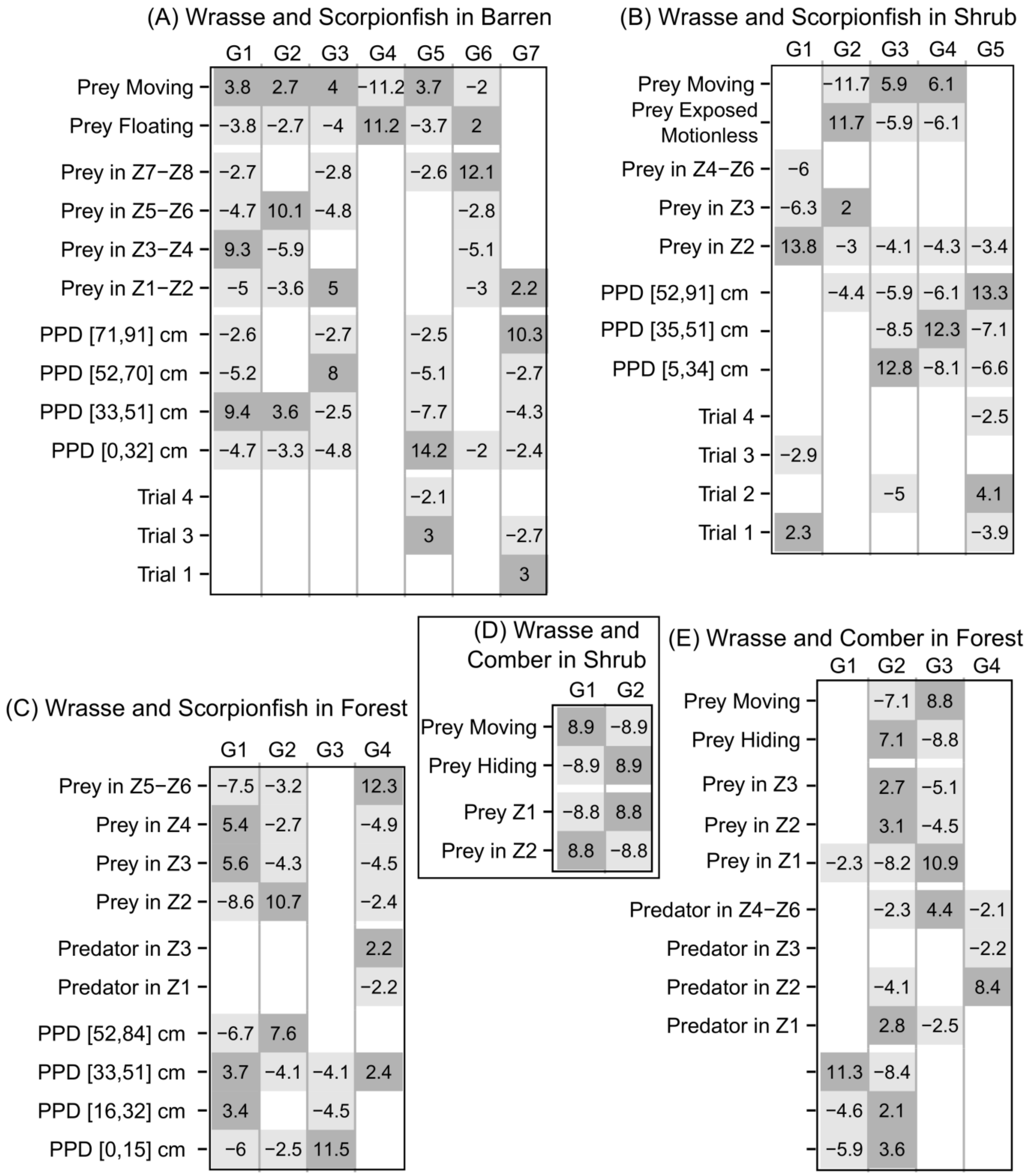


Figure S2. Value tests of the clustering used to detect tendencies between prey and predator respective positioning and activity, and their relative distance. For each prey-predator couple within each habitat (A to E), multivariate behavioral observations were clustered. To assess putative associations (positive or negative) among behavioral categories, value test was carried for each cluster (columns). Behavioral categories (rows) that were under-represented in the given cluster relative to the other clusters (value test significantly negative) are in light grey. Categories that were over-represented (value test significantly positive) are in dark grey.

Wrasse - scorpionfish behavioral interactions

Within barrens, wrasses were moving in every strata of the water column, except for the sub-surface (Z7-Z8). These movements were constrained since wrasses avoided scorpionfish by keeping a great distance from it ([52, 70] cm), especially when wrasses approached the bottom where scorpionfish were always sit on (Figure 6-A and Figure S2-A.G1.G2.G3).

Sometimes wrasses stopped moving for staying exposed motionless, with a preference for doing so in sub-surface (Figure S2-A.G4.G6).

Within shrub, wrasses were moving mainly 10 cm up to the shrubby strata and sometimes further (avoiding Z1 and Z2) by keeping an intermediate distance from scorpionfish ([35, 51] cm), which were always sit within the shrubby strata (Figure 6-B and Figure S2-B.G4). Sometimes, wrasses stopped moving for staying exposed motionless, with a preference for doing so 10 cm up to the shrubby strata (Figure 6-B and Figure S2-B.G2).

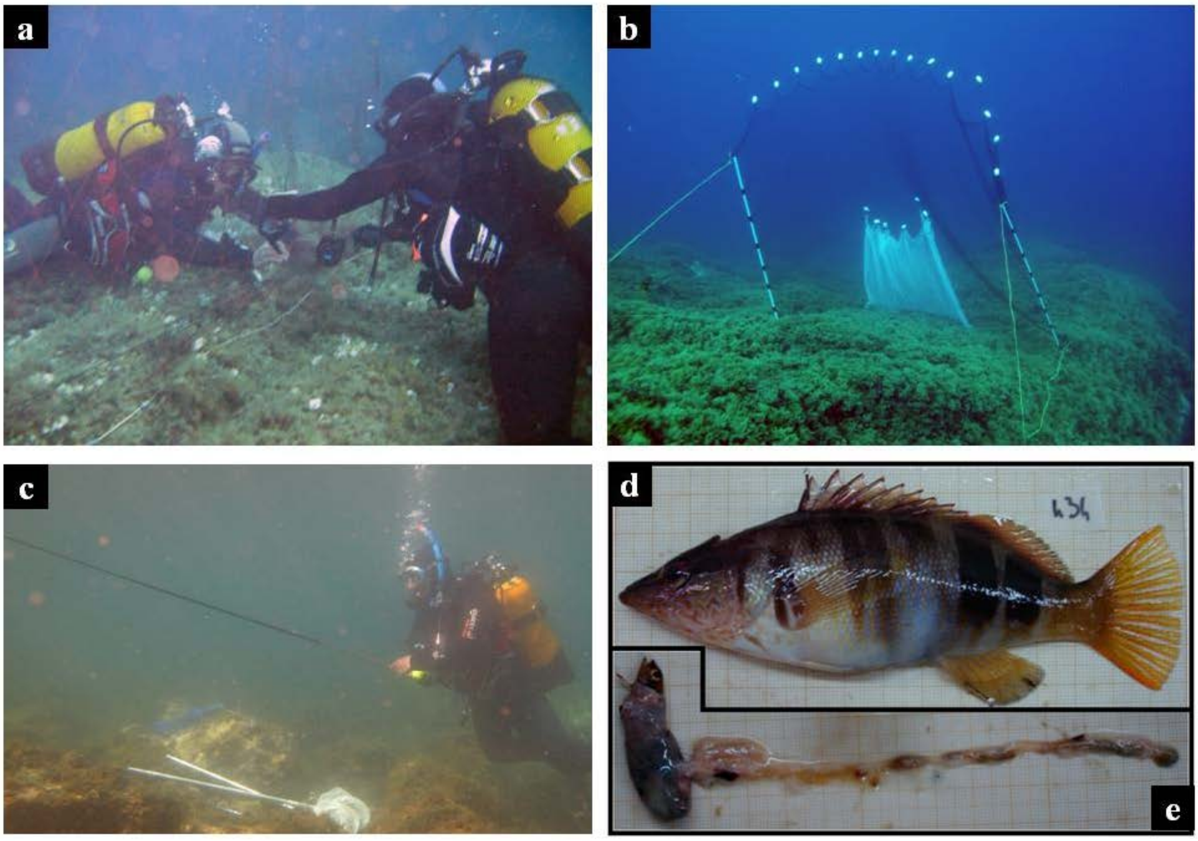
Within forest, wrasses were in the upper-part of the canopy (Z3) and just above (Z4), while being at short to medium distance ([16, 51] cm) from scorpionfish that were laid on the bottom (Figure 6-C1 and Figure S2-C.G1). Wrasses were in the inner canopy (Z2) only when they were far ([52, 84] cm) from scorpionfish (Figure 6-C1 and Figure S2-C.G2). When scorpionfish were sit upon the canopy at the interface with open-water (33% of observations), wrasses maintained intermediate distances ([33, 51] cm) by using sub-surface (Figure 6-C2 and Figure S2-C.G4).

Wrasse - comber behavioral interactions

Within shrub, wrasses were hidden motionless within the shrubby strata during 75% of our observations (Figure 6-D1 and Figure S2-D.G1). They sometimes moved, with a slight preference for moving just above the shrubby strata (15% of our observations) over moving around shrubs (9% of our observations) (Figure 6-D2 and Figure S2-D.G2).

Within forest, wrasses were observed within the canopy (Z2 and Z3) in 86% of our observations, mostly hiding (75%) and sometimes moving (12%), while combers were at short to intermediate distances ([0, 44] cm), between understory and above the canopy (Figure 6-E1 and Figure S2-E.G2). Oppositely, wrasses used the understory (Z1) only for moving (12% of our observations) when combers were in or above the canopy (Figure 6-E2 and Figure S2-E.G3).

Chapter 5. Trophic structure of *Cystoseira brachycarpa* forests, and the diet of macrocarnivorous fish



Sampling gears used for harvesting fish: trammel for catching large sized fish (a), 'funnel' for trapping small-sized fish when we chase them (b), line and hooks for piscivores (c). A *Serranus scriba* collected (d) and its digestive track containing a *Tripterygion delaisi* (e)

This chapter will be refined later and submitted to an international journal, with the co-authors as follow:

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1 Introduction

1.1 Problematics

The food webs of infralittoral ecosystems in the Mediterranean have been little studied. Excepting studies carried out strictly on *Posidonia oceanica* meadow (e.g. Bell & Harmelin-Vivien 1983; Khoury 1987), most of the studies were not from an habitat perspective. They investigated food webs of seascapes composed by both shallow rocky reefs (covered mostly by *Dictyota* sp. and *Halopteris* sp.) and deeper *P. oceanica* meadow (Lepoint *et al.* 2000; Pinnegar & Polunin 2000), or seascapes composed by both sandy sediments covered by brown algae and *P. oceanica* meadow (Vizzini & Mazzola 2004; 2009), or seascapes whose habitat composition was not described (Jennings *et al.* 1997; Deudero *et al.* 2004) since they focused on broad patterns of spatial variations in the food webs. No study investigated the food web of rocky reefs covered by *Cystoseira brachycarpa* forest.

Animal assemblages associated to *Cystoseira brachycarpa* forest, including fish, are more diversified and more abundant compared to animal assemblages associated to other rocky habitats composed by less structurally complex macroalgae (Chapters 2 and 3, and references therein). The role of *C. brachycarpa* in sustaining abundance and diversity of animals may be two-fold. On one hand, *C. brachycarpa* is a highly productive primary producer whose its biomass dominates the macroalgae assemblage in *C. brachycarpa* forest (Chapter 3 and Hoffmann *et al.* 1992). *C. brachycarpa* could be an important source of organic material to the food web, relatively to the other putative sources such as the other benthic primary producers and phytoplankton. On the other hand, *C. brachycarpa* is a habitat-former organism that increases structural complexity of habitat. This may provide shelter to other organisms and putatively stabilize prey-predator lethal interactions between every trophic levels from primary consumers to higher order predator fish (Chapters 2 and 4). Consequently, structural complexity provided by *C. brachycarpa* may contribute to the persistence of populations forming a diversified faunal community associated to *Cystoseira* forest (Janssen *et al.* 2007).

Focusing on fish assemblages associated to *Cystoseira brachycarpa* forests, it includes juveniles and adults of numerous small-sized species, crypto-benthic (*e.g.* Gobiidae, Trypterigidae) and necto-benthic (mainly *Symphodus* spp. and *Coris julis*). Previous studies that investigated their feeding habits in other habitats than *C. brachycarpa* forest found that they feed mainly on small-sized invertebrates (Stergiou & Karpouzi 2002 and references therein). They are therefore usually referred as 'mesocarnivores' (Bell & Harmelin-Vivien 1983; Cresson *et al.* 2014). These mesocarnivorous fish cohabit in *C. brachycarpa* forests with larger-sized fish species (mainly *Serranus cabrilla*, *S. scriba*, and *Scorpaeana porcus*, Chapter 3), which are putative predators of some mesocarnivores. Indeed, these larger-sized fish are known to prey upon both large-sized invertebrates and small-sized fish in other habitats than *C. brachycarpa* forest (Stergiou & Karpouzi 2002 and references therein) and are therefore usually referred as 'macrocarnivores' (Bell & Harmelin-Vivien 1983; Cresson *et al.* 2014). Tank experiments (Chapter 4) highlighted that *Cystoseira* canopy may drastically reduce foraging efficiency of *Serranus cabrilla* and *Scorpaeana porcus*, by providing shelter to *Symphodus ocellatus* (and potentially to other small-sized fish). This stressed the need to estimate macrocarnivores' feeding habits specifically in *C. brachycarpa* forests, in order to assess if macrocarnivores effectively prey upon small-sized fish despite the large availability of shelter for prey fish.

For better understanding the role of *C. brachycarpa* in sustaining its associated faunal community, the present study aimed to:

1/ Describe the global trophic structure in two *C. brachycarpa* forests located few kilometers apart, and to assess consistencies among localities.

2/ Identify what are the sources of organic matter (*e.g.* phytoplankton, *C. brachycarpa*, other benthic primary producers) sustaining the food web.

3/ Estimate feeding habits of macrocarnivorous fish

To achieve these aims, two complementary techniques were used: gut content analysis and stable isotopes composition analysis.

1.2 Theoretical background of the techniques used

1.2.1 Gut content analysis

Gut content analysis is one of the most common methods to study trophic relationships, by providing insights into the dietary composition of organisms such meiofauna (*e.g.* for amphipoda associated to *P. oceanica* meadows: Michel 2011) and macrofauna (e.g. for Mediterranean coastal fish: Bell & Harmelin-Vivien 1983; Harmelin-Vivien *et al.* 1989; Stergiou & Karpouzi 2002 and references therein). The proportional weight (W) of each prey-item (relatively to the total weight of prey found in stomach, or in the whole gut depending on the organism) reflects nutritional importance of prey-items. However, some drawback and biases are inherent to this metric. Weights are not totally valid indicators of nutritional importance since it include the measurement of both digestible and non-digestible material such as crustacean exoskeleton and mollusk shell. This may lead to underestimate the importance of soft-bodied prey, such as fish and squid. Moreover, proportional weight is biased toward prey-items that need longer time to be digested. This may induce underestimation of soft-bodied prey that are usually more rapidly digested. Also, digestion rate is usually higher for larger prey-items, this may lead to underestimate importance of small-bodied prey items (Hyslop 1980 and references therein). Lastly, some predators fragment and grind their food before ingestion rending their different prey items hardly identifiable by gut content analyses. For instance, it is difficult to distinguish planktonic and benthic copepods in gut contents of labrids (Bell & Harmelin-Vivien 1983; Khoury 1987; but see Levi 2004).

1.2.2 Stable isotopes composition analysis

Stable isotopes composition analysis have become a popular method for gaining extra insights into the functioning of littoral food webs, and notably to assess trophic position of organisms into the food web and the relative importance of the different sources of organic material in supporting food web (e.g. for Mediterranean infralittoral zones: Jennings *et al.* 1997; Lepoint *et al.* 2000; Pinnegar & Polunin 2000; Vizzini & Mazzola 2004; 2009).

Stable isotopes analyses applied to ecological studies use most often the ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ (hereafter noted $\delta^{15}N$ and $\delta^{13}C$, respectively). Isotopic composition of an organism is the weighted average of the isotopic composition of its different food sources, modified by the trophic enrichment factors (TEFs). TEF is the net result from isotopic discrimination (*i.e.* the differential comportment of heavy and light isotopes) occurring during biochemical processes, and conducing to isotopic composition differences between the consumer and its food sources. TEFs vary from an element to another. Moreover, TEF for a given element varies between consumers, and depends, among other things, on the consumer species, on life history stage, on the tissue analyzed (*e.g.* liver, muscle), on individual physiology, and on the type of food item (Vanderklift & Ponsard 2003; Caut *et al.* 2009). Consequently, TEFs specific to every single studied-consumer should be ideally estimated by using lab-based feeding experiments, but this is rarely the case due to logistic constraints (Caut *et al.* 2009).

Nevertheless, lab-based feeding experiments highlighted that TEFs are usually more important for $\delta^{15}N$ than for $\delta^{13}C$, ranging broadly between 1.5‰ and 4‰, and between -1.5‰ and 2‰, respectively (Post 2002; Vanderklift & Ponsard 2003; Caut *et al.* 2009). Due to the high TEF for $\delta^{15}N$, *i.e.* the great difference in $\delta^{15}N$ value of a consumer relative to its prey, $\delta^{15}N$ values may help define the trophic levels of organisms. Contrastingly, due to the minimal TEF for $\delta^{13}C$, $\delta^{13}C$ values may help to estimate carbon source inputs to consumer diets (Post 2002 and references therein). For instances, if phytoplankton has lower $\delta^{13}C$ values than benthic primary producers (Dauby 1989), planktonic primary consumers will also have lower $\delta^{13}C$ values than benthic primary consumers, and this differences will be transmitted to the higher trophic levels and enable to distinguish the planktonic and benthic trophic pathways.

However, distinguishing the different trophic pathways is possible only when $\delta^{13}C$ values are different between the primary producers, what is not always the case (e.g. Jennings *et al.* 1997; Park *et al.* 2013). Moreover, isotopic compositions of organisms may exhibit important spatial variations that may be due to spatial variations in their feeding habits, or simply reflect spatial variations in isotopic composition of the same food material due to spatial variations in the starting isotopic compositions of primary producers and detritus that sets up different isotopic baselines (Casey & Post 2011). Spatial variations in isotopic baselines may be due to a large array of phenomena, including for instances (1) site-specific isotopic compositions of nutrients, dissolved inorganic carbon and detritus that may be related to their differential origins (*e.g.* relative inputs from open-sea *vs* terrestrial systems) (Dauby 1989; Vizzini & Mazzola 2004; Vermeulen *et al.* 2011), or (2) site-specific primary producers' trophic enrichment factors due to site-to-site differences in their primary productivity rate, which may be related to differences in the amount of nutrients, or differences in the light intensity affected notably by depth, clearness of water, and the duration of sunshine period (*e.g.* shady *vs* sunny sites) (Lepoint *et al.* 2003; Stutes *et al.* 2006).

For estimating feeding habits of a particular consumer, stable isotope composition analysis has been advocated as a complementary approach to gut content analysis. When a consumer preys upon multiple sources (which is the case for most of coastal fishes), its isotopic compositions is a mixture of the isotopic compositions of its foods sources. Therefore, for reconstructing consumer diets, it is usually necessary to use stable isotope mixing models based on isotopic compositions of consumers and sources tissues. Such approach has three main advantages over gut content analyses. Firstly, consumer isotopic compositions reflect only isotopic compositions of material that were actually digested and assimilated. This allows to better estimate the actual nutritional importance of sources because some materials are ingested but not assimilated (*e.g.* crustacean exoskeleton, mollusk shell). Secondly, isotopic compositions of tissues that have low isotopic turnover rate (*e.g.* white muscle) weigh short-time variations in diet and reflect therefore consumer diet 'averaged' over months (Hesslein *et al.* 1993; Madigan *et al.* 2012; Xia *et al.* 2013), while gut contents give a 'snapshot' picture of consumer's diet. Thirdly, for estimating isotopic composition of putative sources, samples are harvested from their environment. Organisms, in one piece, are therefore easier to identify than organisms found in fragments in gut contents. This may help to assess nutritional importance of some sources that are always unidentifiable in gut contents because found only in fragments (*e.g.* gelatinous plankton consumed by apex predators suchs as *Thunnus thynnus*, Cardona *et al.* 2012).

However, some drawbacks are inherent to stable isotope mixing models. When some distinct sources have overlapping isotopic compositions, this may be impossible to estimate their relative importance. Moreover, depending upon the geometry of the system, *i.e.* the relative position of consumers and sources into the isotopic space, estimated distributions of sources' proportional contribution may remained underdetermined (multimodal distributions), what limits interpretation of model-output to a listing of the most likely scenario as regards proportional contributions of each source (Semmens *et al.* 2013). Finally, isotopic mixing model are sensitive to the values of trophic enrichment factors that are inputted (Bond & Diamond 2010). Model estimations may be altered by the use of inaccurate TEFs values, for instance when TEFs values specific to the studied organisms are not available. Nevertheless, in such case, a common acceptable practice consists in using TEFs values of the most similar organisms (usually found in the literature, e.g. Vanderklift & Ponsard 2003; Caut *et al.* 2009) and in fitting Bayesian isotopic mixing models (*e.g.* SIAR model, Parnell *et al.* 2010) whose the Bayesian approach allows to consider the inaccuracy of the inputted TEFs values.

2 Material and Methods

2.1 Ethic statements

The sampling activity did not involve endangered or threatened species according to the Annexe II (amendment into force during the sampling activity: Marrakesh, 2009) of the 'Protocol Concerning Specially Protected Areas and Biological Diversity in the Mediterranean' (Barcelona, 1995), excepting *Cystoseira brachycarpa*. No collection within any marine protected area was performed. The experimental harvesting protocol by scuba-diving was approved by 'Direction interrégionnale de la mer Méditerranée' (the French administration in charge of the Maritime affairs) by the permit released on 2011 April 8th. The experimental fishing by trammel was approved by '*Prud'homie* de Calvi - Iles Rousses' (the organization in charge of the local Community Based Resource Management). After collection, all efforts were made to minimize pain when killing animals. Invertebrates were frozen (-20°C) directly from state of alive. Fish caught alive were killed by anesthesia (Quinaldine) overdose, following the Directive 2010/63/EU of the European Parliament and of the Council.

2.2 Study sites

Food web of *Cystoseira brachycarpa* forests was investigated in two study sites located in NW Corsica, one site outside the Revellata Bay and one site within the Revellata Bay (Figure 1). Both sites extended on 80 x 20 m², between -5 m and -10 m depth. Sea bottom slope was gentle (0° to 15°). Substrate was only monolithic rock (as opposed to boulders, pebbles etc.), with low substrate roughness (*i.e.* few steps and crevasses) and almost no sun-shading structures (*e.g.* overhang). Macroalgae assemblage was dominated by *Cystoseira brachycarpa* (> 90% of total macroalgal biomass) that formed dense and continuous canopy around 15 to 20 cm in height, which covered more than 80 % of each study site. Habitats were therefore highly similar in both sites.

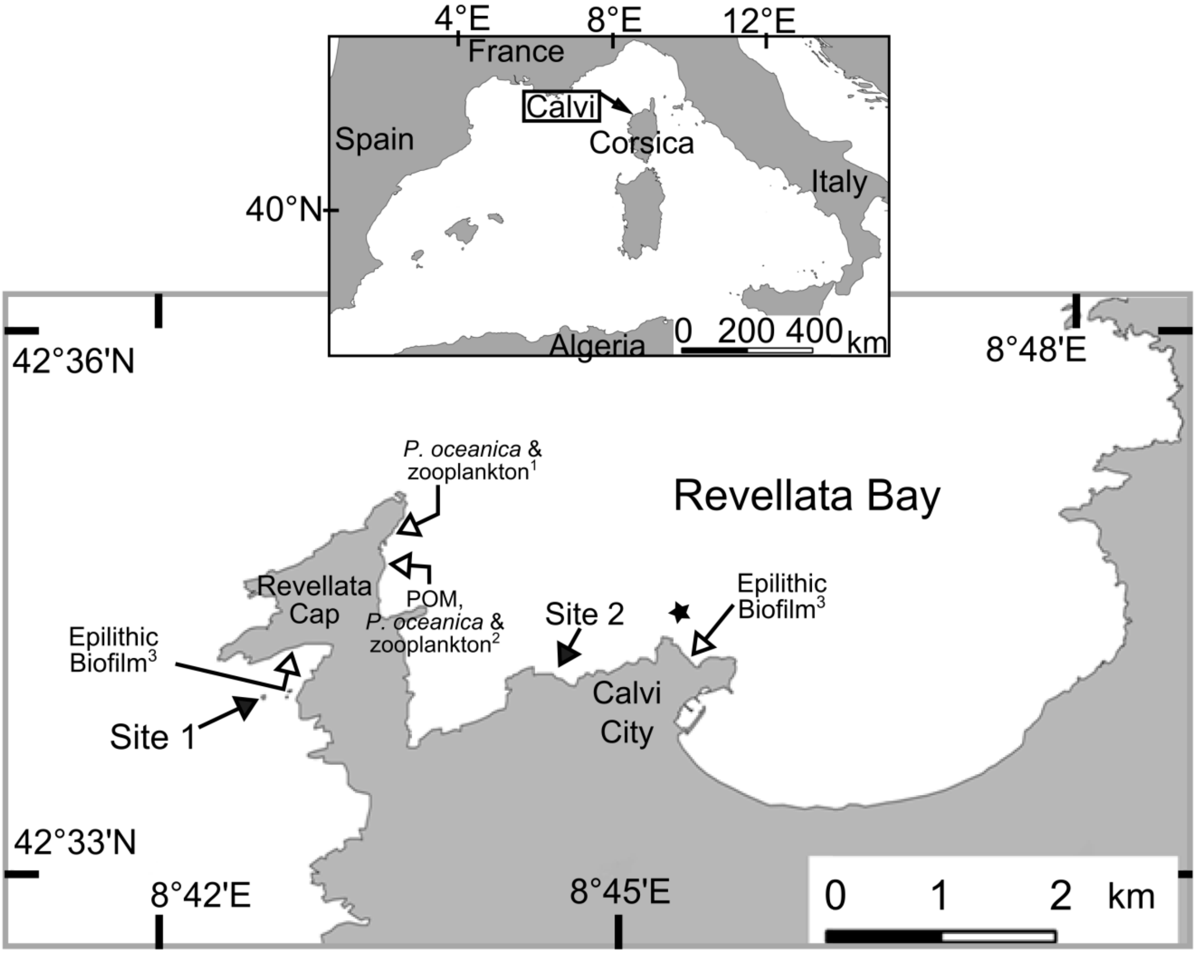


Figure 1: Localization of the study area. Black filled arrows indicate the 2 sites sampled in this study. White filled arrows indicate the study sites of (1) Pinnegar and Polunin 2000, (2) Lepoint *et al.* 2000, and (3) Vermeulen *et al.* 2011, whose some isotopic data were collected for comparing with the present-study data set. The star symbol spot the sewage outfall of Calvi City.

However, we cannot exclude some differences between the two sites that may induce differences in their food web structure, or at least in isotopic composition of organisms through a shifting baseline. Adjacent habitat-types were different. The site outside the bay was a rocky platform surrounding (like a belt) a mountain-like islet, and thereafter the platform breaks suddenly toward deepest coralligenous habitat-types. Contrastingly, the site inside the bay was continued from 10-12 m deep by an extended *Posidonia oceanica* meadow. Moreover, the site outside the bay is more exposed to high sea and to strong waves especially during winter storms (pers. com. from local peoples), and receive less direct sunlight on morning, due to its westward position relative to the high cliffs of the Revellata Cap (Figure 1). Within the Revellata Bay compared to outside, two seasonal rivers increase input of nutrients and detritus derived from terrestrial environment (Dauby 1989). Moreover, there is inside the Bay the Calvi City and its sewage outfall, and an off-shore fish farm.

2.3 Sample collection and preparation for isotopic ratios measurements

All samples were collected between 2011 September 2nd and 23th, in daylight hours. The studied organisms were divided by categories (hereafter referred as 'trophic entities', Table 1) that were based on the combination of taxa and body-size class (*e.g. Symphodus ocellatus* [16,38] mm Total Length) or solely on the taxa (*e.g. Dictyota* spp.). In order to study organisms that inhabit permanently in the study site, we selected trophic entities that have small home range relatively to the extent of the study sites. This excluded notably large transient fish such as *Dentex dentex*. For harvesting organisms inhabiting exactly in the study sites, scuba (or snorkel) diving was used as long as possible. We tried to sample each trophic entity in both sites. Only few trophic entities were sampled only in one site (Table 1). After collection, samples were frozen (-20°C) as soon as possible, for later sorting and preparation at the laboratory.

Macroalgae (also referred as 'benthic primary producers', depending on the context) were picked-up from the substrate and stored individually in ziplock bags. Each macroalgae individual was scraped clean of epiphytes using a scalpel blade, and kept whole for constituting (individual-specific) replicates (6 per sites). *Cystoseira brachycarpa* individuals were composed by both old branches (brown colored) and young branches (green colored) that grew since winter and since summer, respectively (Hoffman et al 1992). These two types of tissues were therefore analyzed separately since they may have integrated temporal variability of nutrients isotopic composition on two different time-scales. Each replicate was the last 5 cm of a branch extremity. Replicates were collected on different individuals.

Suspended particulate organic matter (POM) was used as a proxy for phytoplankton. Each POM replicate (8 per site) was obtained by filtering 4.8 L of seawater on GF/F Whatman® Filters (diameter: 47 mm, retention: 0.7 µm), after pre-filtering on a 200 µm sieve. Seawater was collected 50 cm above the substrate by scuba. Hereafter, 'primary producers' refers to both Macroalgae and POM.

Benthic macroinvertebrates were harvested by using the scuba-operated 1m² 'Enclosed Anesthetic Station' (EAS, see chapter 3 for full description of the method). Macroinvertebrates were sorted by trophic entities based on the combination of operational taxonomic units and body-size classes obtained by sieving (*e.g.* Caridae [1,2[mm, see list in Table 1). All macroinvertebrate individuals were kept whole, excepting Gastropoda whose shell was removed. One replicate for a given trophic entity was obtained by pooling all individuals that were harvested in the same 1m² EAS sample and that belonged to the trophic entity considered. Considering all individuals collected in 1m² rather than an *a priori* subset (*e.g.* a given number of individuals belonging to a given species), intended to obtain replicates that were representative of the assemblage. A total of 6 replicates per trophic entity and per sites were constituted.

Primary producers

FG	**Site**
Particulate organic matter	1&2
Articulated corallinales	1&2
Cystoseira brachycarpa (old branches)	1&2
Cystoseira brachycarpa (young branches)	1&2
Dictyopteris spp.	1&2
Dictyota spp.	1&2
Flabellia spp.	1&2
Halopteris spp.	1&2
Padina spp.	1&2
Peyssonnelia spp.	1&2

Fish

Taxa	**Total length in mm**	**Beh.**	**Diet**	**Site**
Bleniidae	[18,24]	CB	Om	1
	[27,33]	CB	Om	1
Coris julis (Cor_jul)	[22,39]	NB	Me	1&2
	[87,137]	NB	Me	1&2
Gobiesocidae	[12,13]	CB	Me	1
Gobiidae	[14,21]	CB	Me	1&2
Scorpaena notata (Sco_not)	[69,158]	CB	Ma	1
Scorpaena porcus (Sco_por)	[82,196]	CB	Ma	1&2
Serranus cabrilla (Ser_cab)	[40,74]	NB	Ma	1&2
	[112,142]	NB	Ma	1
Serranus scriba (Ser_scr)	[41,65]	NB	Ma	1&2
	[125,170]	NB	Ma	1&2
Symphodus ocellatus (Sym_oce)	[16,38]	NB	Me	1&2
	[45,53]	NB	Me	2
	[60,73]	NB	Me	1&2
Symphodus roissali (Sym_roi)	[33,51]	NB	Me	1&2
	[59,82]	NB	Me	1&2
Symphodus tinca (Sym_tin)	[165,194]	NB	Me	1&2
Trypterigion delaisi (Try_del)	[27,51]	CB	Me	1&2

Invertebrates

FG	**Body size in mm**	**Loc.**	**Site**
Zooplancton	[0.2,0.5[		1&2
	[0.5,1[		1&2
Gastropoda	[2,4[	W	1&2
	[4,8[	W	1&2
	[8,+[	W	1&2
Amphipoda	[1,2[	CS	1&2
	[2,4[	CS	1&2
Caridea	[1,2[	CS	1&2
	[2,4[	CS	1&2
	[4,8[	CS	1&2
	[8,+[	CS	1
Isopoda	[2,4[	CW	1&2
Galatheoidea	[2,4[	CW	1&2
Majidae	[2,4[	CW	2
	[4,8[	CW	1&2
	[8,+[	CW	1&2
Paguroidea	[1,2[	CW	1&2
	[2,4[	CW	1&2
	[4,8[	CW	1&2
	[8,+[	CW	2
Other Brachyura	[4,8[	CW	1&2

Table 1. Trophic entities, sampled in Site 1 and/or 2. Numbers within brackets indicate minimum and maximum sizes of organisms. For invertebrates, manner of locomotion (Loc.) is walker (W) or Swimmer (S) and the C indicate Crustacean. For fish, behavior (Beh.) is crypto-benthic (CB) or necto-benthic (NB). Diet is Omnivore (Om), Mesocarnivore (Me) or Macrocarnivore (Ma), according to Bell & Harmelin-Vivien(1983). Abbreviations subsequently used for the names of fish species are indicated.

Small sized crypto-benthic fish (*e.g. Trypterigion* spp.) were also sampled by EAS. Small sized necto-benthic fish (*e.g.* small labrids) were collected by scuba using hand nets. Larger necto-benthic fish (*e.g. Symphodus tinca*, *Serranus* spp., *Scorpaena* spp.) were collected by using several methods depending on their life history traits: hook and line (operated by scuba or from the boat anchored in the middle of the study site), spear fishing (by snorkel) and bottom trammel net (dropped from the boat and finely positioned by scuba). Fish were sorted by trophic entities based on operational taxonomic units (from family to species depending on the life stage and crypticism, see Table 1) and by classes of body-size (total length, TL) (*e.g.* Blenniidae [18,24[mm). Every replicate was composed by a single fish individual. For most of fish trophic entities, only dorsal white muscle tissue was kept, since white muscle tends to be less variable in terms of $\delta^{13}C$ and $\delta^{15}N$ values than other tissues (Pinnegar & Polunin 1999). For very small sized individuals (usually < 20 mm TL), all muscles and bones (mainly calcium phosphate) of the posterior body-part was kept after the skin and scales (mainly calcium carbonate) was removed (Frédérich *et al.* 2010).

Mesozooplankton was obtained using a net with a mesh of 200 µm, towed in sub-surface (during 20 min at 1 kn) all around the study site, at 7AM due to logistic constraints. Mesozooplankton sample was sieved for obtaining one replicate per site of Zooplancton [0.2,0.5[and Zooplancton [0.5,1[(mm). Zooplankton were the only samples that were collected in, but also around, the study sites, because the surface required for maneuvering the boat while towing the net, was larger than the extend of the study site.

2.4 Isotopic ratios measurements

All samples were oven-dried for 48 h at 50 °C and ground to a fine powder. After grinding, samples containing inorganic carbonates (all invertebrates and the macroalgae *Padina* sp. and articulated corallinales) were split in two. Half of the powder was acidified (HCl 37% during 24H) and used for assessing $\delta^{13}C$ values. The other part of the powder was not acidified and used for assessing $\delta^{15}N$ values (Pinnegar & Polunin 1999). Powders were loaded into tin capsules (around 3 mg for macroalgae and 1 mg for animals). Isotopic measurements (^{12}C, ^{13}C, ^{14}N and ^{15}N) were performed with a C-N elemental analyzer (Vario Microcube, Elementar, Germany) coupled to mass spectrometer (Isoprime100, Isoprime, UK). The isotopic data were expressed as delta values ($\delta^{13}C$ and $\delta^{15}N$, in ‰), relative to the VPDB (Vienna Peedee Belemnite) and to atmospheric N2, for carbon and nitrogen respectively. Certified isotopic reference materials were IAEA CH-6 (sucrose, $\delta^{13}C$ = -10.4 ‰ ± 0.2 ‰) and IAEA N2 ($\delta^{15}N$ = 20.3 ‰ ± 0.2 ‰). Glycine was used as elemental standard (31.99 % C, 18.72 % N) and laboratory standard for stable isotopes. The standard deviations of repeated measurements (n = 102) on glycine were 0.23 ‰ for $\delta^{13}C$ and 0.24 ‰ for $\delta^{15}N$. Lipid contents may affect isotopic composition of tissue since lipid are generally highly depleted in ^{13}C compared to diet, as a consequence of animal lipid metabolism. The $\delta^{13}C$ values of samples that had a C:N ratio higher than 3.5 were corrected to account lipid content following the equation of Post et al (2007):

$$\delta 13C_{Corrected} = \delta 13C_{Untreated} - 3.32 + 0.99\frac{C}{N}$$

2.5 Stomach contents of macrocarnivorous fish

Digestive tracks of all macrocarnivorous fish individuals ((sub-)adults of *Serranus cabrilla*, *S. scriba*, *Scorpaena notata* and *S. porcus*) were removed as soon as possible after fish were caught, just before freezing samples for later isotopic measurements. Digestive tracks were fixed during 24H in formaldehyde (3%) isotonic solution, and then stored in alcohol (70%). Only prey-items contained in the stomach were recorded. They were sorted into the same groups (trophic entities) than those considered for isotopic measurements. The importance of the different prey-types in the diet of each species was described using 3 indices calculated on all non-empty stomachs. The prey-item % frequency (F) was the number of stomach containing the prey with respect to the number of non-empty stomachs analyzed. For each stomach, the % number (N) of each prey-type was calculated as the number of prey items belonging to the specific prey-type with respect to the total number of prey items contained in the stomach. Similarly, the % weight (W) was the wet weight (to the nearest 0.01g) of the pool of individuals belonging to the specific prey-type with respect to the total weight of all prey items. Prey-types frequencies F emphasize predator population-wide food habits. The % numbers N (also referred as numerical importance) emphasizes feeding behavior. The % weights W (also referred as weight importance) emphasizes, to some extent, nutritional importance of prey-items (Hyslop 1980).

2.6 Statistical analyses

2.6.1 Global analyses of isotopic compositions

In order to compare the patterns of isotopic compositions between the 2 study sites, Mantel tests and permutational analyses of variance (PERMANOVAs) were used on all 3 trophic compartments, and separately for primary producers, invertebrates and fish. For Mantel tests, Euclidean distance matrix between pairs of trophic entities was computed for each site, on normalized $\delta^{13}C$ and $\delta^{15}N$ mean values. Mantel test tested the null hypothesis of no correlation (Pearson's product-moment correlation) between the two matrices. A reject of the null hypothesis indicates that the two matrices are correlated, *i.e.* there are similarities between sites in the pairwise distances among trophic entities. Perfect correlation ($r = 1$) may arise in two different cases: (1) each trophic entity have similar isotopic composition in both sites, or (2) isotopic compositions of all trophic entities vary similarly across sites and consequently the pairwise distances among trophic entities are conserved across sites. In both cases, this indicates that the trophic structure of *C. brachycarpa forest* is similar in both sites since the positions of trophic entities relative to each other are similar. Two-way crossed multivariate PERMANOVAs were used for testing the differences in isotopic compositions between trophic entities and sites, and therefore for distinguishing the 2 cases enunciated above. Euclidean distance matrix was computed on normalized $\delta^{13}C$ and $\delta^{15}N$ values. The fixed factors were Trophic Entity and Site. Univariate PERMANOVAs were also used on $\delta^{13}C$ and $\delta^{15}N$ separately, in order to identify which isotopic ratio drive multivariate differences (if any). When the 3 terms of the PERMANOVAs (*i.e.* including the interaction term) were significant, this indicated that the effect of Site depended upon the Trophic Entity, or in other words that trophic entities did not all vary homogeneously across the two sites. Hierarchical clustering on the differences in isotopic compositions across sites was used in order to identify groups of trophic entities that varied homogeneously across sites. PERMANOVAs were subsequently performed on each of these groups for controlling the absence of interactions between Trophic Entity and Site.

For gleaning a global picture of the trophic structure of *C. brachycarpa* forest beyond the site-to-site differences, groups of trophic entities that had (in average over sites) similar isotopic compositions were obtained by using hierarchical clustering. Ward's method was used on the Euclidean distance matrix computed on normalized $\delta^{13}C$ and $\delta^{15}N$ mean values averaged over the 2 study sites. This was performed separately for primary producers, invertebrates and fish.

For fish, in order to test the putative monotonous relationships between body-length (TL) and $\delta^{13}C$ values and between TL and $\delta^{15}N$ values, irrespectively of the taxa, Spearman's rank correlation tests were used for each site separately. The variables were mean body length and mean isotopic compositions per fish trophic entity (*i.e.* taxa x size class).

2.6.2 Feeding habits of macrocarnivorous fish

Stomach contents were compared between the macrocarnivorous fish species by using one way PERMANOVA, with the fixed factor Species. For *S. scriba*, non-empty stomachs were available in both sites (see Results). Their contents were compared between the 2 sites by using one way PERMANOVA, with the fixed factor Site. For both PERMANOVAs, the statistical unit was the stomach (only non-empty ones). The response variables were both %N and %W for all prey-items, and the dissimilarity measure used was Bray-Curtis. For each macrocarnivore species, the relative importance of the different prey-items was visualized by using biplots (x = % N, y = % W).

Relative positions and overlap of the isotopic niches of the 4 macrocarnivores (*i.e.* in the biplot ($x = \delta^{13}C$, $y = \delta^{15}N$), the areas covered by their δ-values) were visually investigated by using standard ellipses, which is to bivariate data as SD is to univariate data (*i.e.* standard ellipse delimits around 68% of the values sampled in a bi-normal distribution). For comparing isotopic niche widths, we used the Bayesian estimations of the Standard Ellipse Area corrected for small sample sizes (SEAc, Jackson *et al.* 2011).

Bayesian stable isotope mixing models were used for estimating dietary proportions of each macrocarnivorous fish species, in each site separately. Models were fitted using the R package 'Stable Isotope Analysis in R' (SIAR, Parnell *et al.* 2010). SIAR models estimate probability distributions of multiple source (prey isotopic compositions) contributions to a mixture (predator isotopic compositions) while accounting for the observed variability in source and mixture isotopic compositions, and in trophic enrichment factors. Sources were selected based on our stomach content analyses. All prey items that had mean weight importance $W \geq 5$ % were included as sources into SIAR model. Sources that had similar isotopic compositions were pooled (according to a hierarchical clustering) for reducing number of sources (Phillips & Gregg 2003) and simplifying the geometry of the system (*i.e.* the relative position of consumers and sources into the isotopic space). This aimed ultimately to better constraint the model solutions, *i.e.* decrease multi-modality in posterior distributions. For the same purpose, prior information was included into the SIAR models: distributions (mean and SD) of %W of (eventually pooled) prey-items were input as prior distribution of dietary proportions (Semmens *et al.* 2013 and references therein). For *S. cabrilla*, some sources not found in stomach contents but shown as putatively important by the review of Stergiou & Karpouzi (2002), were included into the model with a prior estimation of 0.1%. This intended to consider that the absence of these prey-items in the few stomach analyzed (n = 4) was not a strong evidence for their null contribution into *S. cabrilla* diet. For all models, Trophic enrichment factors (TEFs) were 1.0‰ ± 0.4‰ SD for $\delta^{13}C$, and 3.4‰ ± 1.1‰ for

$\delta^{15}N$ (Post 2002). For each SIAR model, we ran 500,000 iterations with an initial discard of the first 50,000 (Parnell *et al.* 2010).

The high number of distinct sources included into the models complicated the geometry of the system. This leads to interrelations among estimations of sources proportional contributions, where the estimated proportional contribution of one source necessarily affects the one of the other sources (co-variations in distributions). Draftsman's plots were used to visualize interrelations between pairs of sources. Interrelations among sources dramatically increased the number of unique possible solution, and distributions of the solutions were sometimes multi-modal (underdetermined). Resulting posterior distributions of each source's proportional contribution were therefore summarized by using violin plots (smoothed distributions), in complement to the usual boxplots. This allowed to appreciate the different mode of the distributions that are as many likely mutually exclusive scenario, which cannot be appreciated by single value such as the median value (Semmens *et al.* 2013).

For gleaning a more global picture of macrocarnivorous fish dietary proportions, proportional contribution of sources were combined *a posteriori* by functional groups (for each model iteration). This also helped in output interpretations by reducing the amount of multi-modality in (combined) distributions since within-functional-group sources interrelations had no effect anymore. For other caveats and assumptions when applying SIAR models, see Parnell *et al.* (2010) and Semmens *et al.* (2013).

For all univariate and multivariate PERMANOVAs, marginal sums of square (type III) were used since designs were unbalanced, and p-values were obtained using 9999 permutations under the reduced model. For all PERMANOVAs that detected some differences, the PERMDISP routine was subsequently performed in order to test if differences were in terms of location and/or dispersion. PERMANOVAs and PERMDISP were performed using the PRIMER 6 and PERMANOVA + B20 package (Clarke & Gorley 2006; Anderson *et al.* 2008). All other tests and all graphical visualizations were performed in R Environment (R Development Core Team 2013) using the libraries vegan (Oksanen *et al.* 2012), SIAR (Parnell *et al.* 2010) and ggplot2 (Wickham 2009).

3 Results and preliminary discussion

3.1 Global trophic structure of *Cystoseira brachycarpa* forests

When considering all trophic compartments, the matrices of distances between pairs of trophic entities computed for site 1 and 2 were highly correlated (Mantel test: $r = 0.88$, $p < 0.001$). This indicated that position of trophic entities relatively to each other, *i.e.* the structure of the trophic system, were globally similar in both sites, and therefore that isotopic compositions averaged over sites were representative of this global structure (Figure 2).

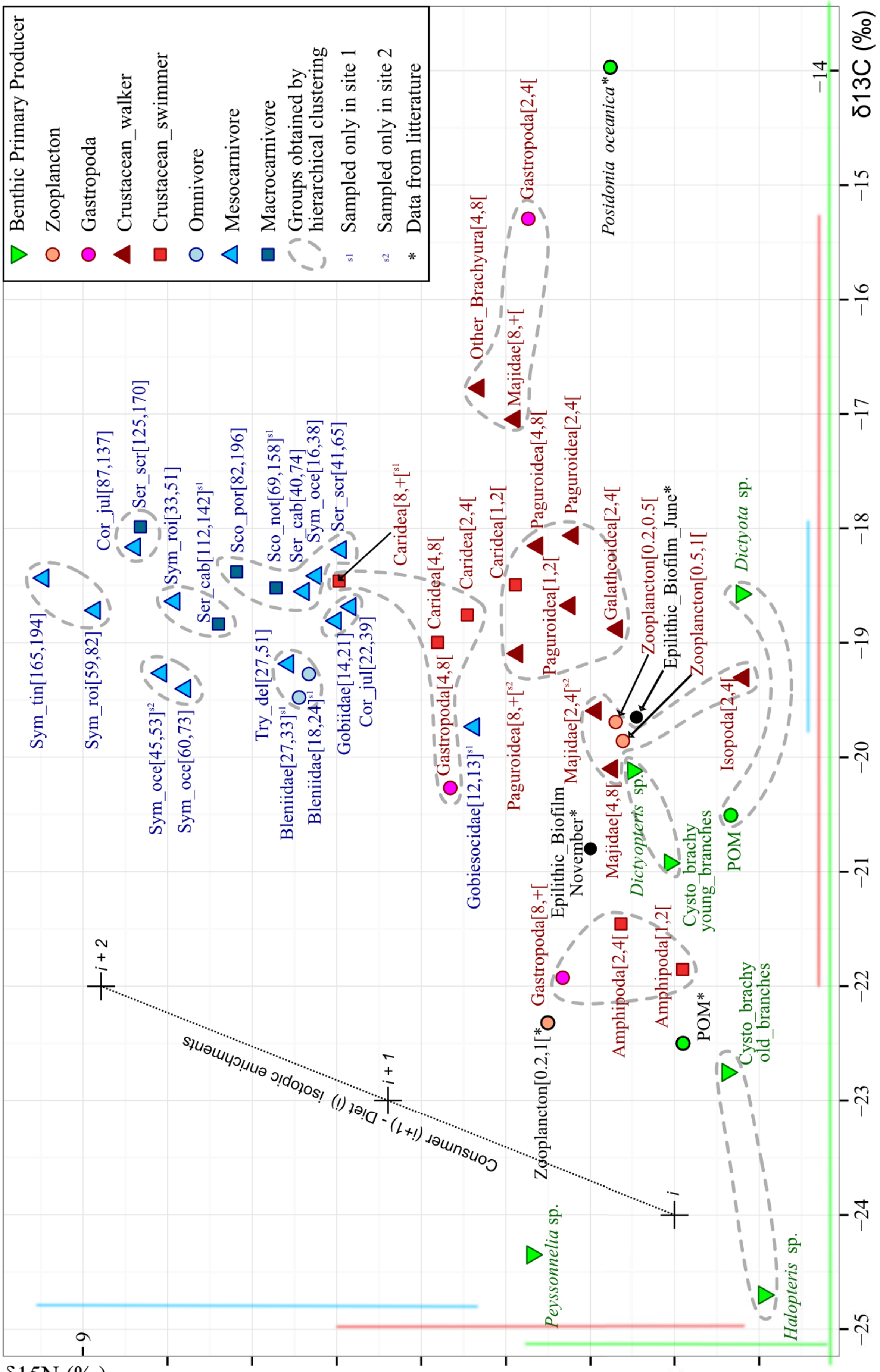

Benthic Primary Producer
Zooplancton
Gastropoda
Crustacean_walker
Crustacean_swimmer
Omnivore
Mesocarnivore
Macrocarnivore
Groups obtained by hierarchical clustering
Sampled only in site 1
Sampled only in site 2
Data from litterature
δ13C (‰)
δ15N (‰)
Consumer (i+1) - Diet (i) isotopic enrichments
Posidonia oceanica*
Peyssonnelia sp.
Halopteris sp.
Dictyota sp.
Dictyopteris sp.
Cysto_brachy young_branches
Cysto_brachy old_branches
POM
POM*
Epilithic_Biofilm_June*
Epilithic_Biofilm November*
Zooplancton[0.2,1[*
Zooplancton[0.2,0.5[
Zooplancton[0.5,1[
Gastropoda[2,4[
Gastropoda[4,8[
Gastropoda[8,+[
Other_Brachyura[4,8[
Majidae[8,+[
Majidae[4,8[
Majidae[2,4[s2
Paguroidea[4,8[
Paguroidea[2,4[
Paguroidea[1,2[
Paguroidea[8,+[s2
Galatheoidea[2,4[
Isopoda[2,4[
Caridea[8,+[s1
Caridea[4,8[
Caridea[2,4[
Caridea[1,2[
Amphipoda[2,4[
Amphipoda[1,2[
Sym_tin[165,194]
Sym_roi[59,82]
Sym_roi[33,51]
Sym_oce[45,53]s2
Sym_oce[60,73]
Sym_oce[16,38]
Cor_jul[87,137]
Cor_jul[22,39]
Ser_scr[125,170]
Ser_scr[41,65]
Ser_cab[112,142]s1
Ser_cab[40,74]
Sco_por[82,196]
Sco_not[69,158]s1
Try_del[27,51]
Blenidae[27,33]s1
Bleniidae[18,24]s1
Gobiidae[14,21]
Gobiesocidae[12,13]s1

Figure 2 (Left-hand page). $\delta^{13}C$ and $\delta^{15}N$ values averaged over the 2 sites. See Table 1 for meaning of abbreviations. Green labels: primary producers; red labels: invertebrates; blue labels: fish. Colored horizontal and vertical lines in the margins indicate their respective ranges of $\delta^{13}C$ and $\delta^{15}N$ mean values. Primary producers that had extreme $\delta^{13}C$ mean values (see Figure 4) had been excluded: *Flabellia* sp. (extremely low), and articulated corallinales and *Padina* sp. (extremely high). Trophic entities labeled in black and marked with '*' were collected from Lepoint *et al.* (2000), Pinnegar & Polunin (2000) or Vermeulen *et al.* (2011), and were not included into clustering. Black dotted line indicates the theoretical trophic enrichment factors from Post (2002).

Primary producers' $\delta^{13}C$ mean values ranged between -31.49 ‰ and -10.04 ‰, and $\delta^{15}N$ mean values ranged between 0.14 ‰ and 3.69 ‰. Hierarchical clustering suggested 6 groups (Figure 2), which were consistent across sites (see below). Most of the putative sources of organic matter had $\delta^{13}C$ mean values ranged between -25 and -18.5 ‰. Isotopic compositions did not allow to differentiate the benthic primary producers from the pelagic primary producers. *Cystoseira brachycarpa* old branches (that grew since winter) were clustered with *Halopteris* sp., and had similar $\delta^{13}C$ values with the one of particulate organic matter (POM) estimated by Lepoint et al (2000) from February to October. *C. brachycarpa* young branches (that grew since Summer) were clustered with *Dictyopteris* sp., and had similar $\delta^{13}C$ values with the one of POM estimated by ourselves (in September like all the other estimations we did). Our estimation of POM was clustered with *Dictyota* sp. It is worth noting that the primary producers thriving in *C. brachycarpa* ecosystem had lower $\delta^{13}C$ mean values than *Posidonia oceanica* (values from Pinnegar and Polunin 2000, and Lepoint et al 2000), excepting the group composed by the articulated corallinales and *Padina* sp.

Invertebrates $\delta^{13}C$ mean values ranged between -21.93 ‰ and -15.3 ‰, and $\delta^{15}N$ mean values ranged between 1.19 ‰ and 5.97 ‰. Hierarchical clustering suggested 5 groups (Figure 2) but they must be regarded with cautious since some were inconsistent across sites (see below). Some clusters were based on Taxonomical groups. For instances, Paguroidea of all size classes were clustered together, like Amphipoda, Zooplankton and Caridea (excluding the smallest < 2mm). For Brachyura, taxonomy and body-size interacted since small and medium Majidae were clustered separately from the large Majidae and other medium Brachyura. The effect of body size was particularly pronounced for Gastropoda, mainly on their $\delta^{13}C$ mean values, which were from very high for small sized ([2,4[) to very low for large sized Gastropoda ([8,+[). There was no evidence for an effect of the manner of locomotion since Swimmer and Walker isotopic values were interspersed. Isotopic compositions did not allow to differentiate benthic invertebrates from pelagic invertebrates. Zooplankton [0.2,0.5[and [0.5,0.1[were clustered with Majidae [2,4[and [4,8[, and Isopoda [2,4[. These trophic entities had not a marginal position along the $\delta^{13}C$ axis, being surrounded on both sides by some other trophic entities. However, it is worth noting the isotopic composition of zooplankton [0.2,1[measured by Lepoint et al (2000) and Pinnegar and Pollunin (2000) (between February and October), were more depleted in ^{13}C.

Fish $\delta^{13}C$ mean values ranged between -19.73 ‰ and -17.99 ‰, and $\delta^{15}N$ mean values ranged between 4.38 ‰ and 9.47 ‰. Hierarchical structuring suggested 8 groups (Figure 2) that were quiet consistent across site (see below). Fish were not clustered by feeding group, since the macrocarnivorous species were positioned intermediately along the $\delta^{15}N$ axis, between some more ^{15}N-depleted and some more ^{15}N-enriched mesocarnivores.

Body length (TL) affected fish isotopic compositions, irrespectively of fish taxonomy. Significant (or closely significant) monotonous relationships were detected in both sites, between $\delta^{13}C$ values and TL and between $\delta^{15}N$ values and TL (Spearman's rank correlation tests reported in Figure 3). Hence, both $\delta^{13}C$ and $\delta^{15}N$ values globally increased with fish body-length (Figure 3). However, it is worth noting that *Symphodus roissali* individuals were particularly enriched in ^{15}N relatively to their body-length, and inversely *Scorpaeana porcus* individuals were particularly depleted in ^{15}N relatively to their body-length. *Symphodus ocellatus* [60,73] were more ^{13}C-depleted relatively to their body length, but only in Site 1.

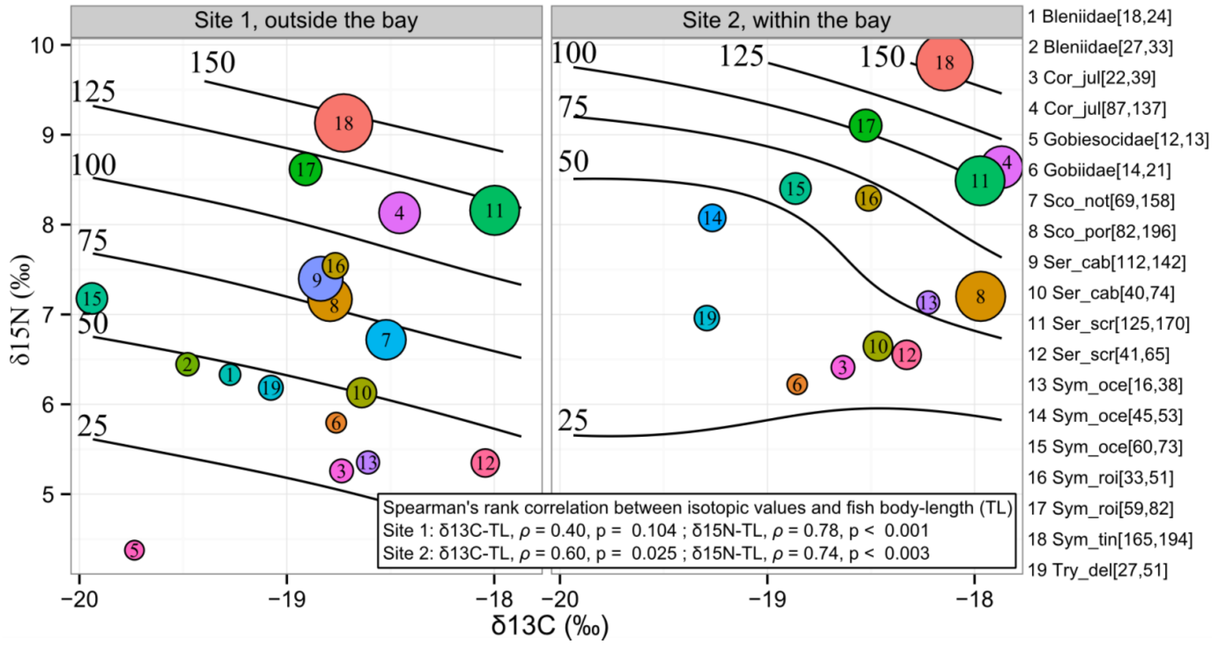


Figure 3: Relationships between fish body-length and $\delta^{13}C$ and $\delta^{15}N$. Points represent $\delta^{13}C$ and $\delta^{15}N$ mean values of taxa-size class (see Table 1 for abbreviations). Point size is proportional to mean body-length (total length in mm). Contour lines represent the smooth response surface of fish body-length over the limits of the biplot, which was obtained by using General Additive Model. Results of Spearman's rank correlations are embedded in the Figure.

3.2 Differences between sites in isotopic compositions

3.2.1 Primary producers

When considering only primary producers, the matrices of distances between pairs of trophic entities computed for site 1 (outside the bay) and 2 (within the bay) were highly correlated (Mantel test: $r = 0.77$, $p < 0.001$). This indicated that the positions in isotopic space of trophic entities relatively to each other, were globally similar in both sites. Despite the clouds of isotopic compositions of sites 1 and 2 were similarly structured, they were located differently due to a global translation (Figure 4). All trophic entities had both $\delta^{13}C$ and $\delta^{15}N$ mean values that increased from site 1 to site 2 (Table S1). Mean increases averaged over trophic entities (the site effect) were 1.06 (0.50) ‰ (SE) in $\delta^{13}C$ mean values and 1.63 (0.29) ‰ in $\delta^{15}N$ mean values. However, all trophic entities did not homogeneously vary across sites, since the terms Trophic Entity x Site were significant in the PERMANOVAs (Table S2). Hierarchical clustering on differences in isotopic compositions across sites suggested 3 groups of trophic entity that varied differently across sites. Variations differed in order of magnitude, not in direction. The group composed by the articulated corallinales, *Flabellia* sp. and *Peysonnelia* sp. had the lowest variations (0.74 (0.53) ‰ for δ^{13}C, 0.42 (0.09) ‰ for δ^{15}N, from site 1 to site 2). *Halopteris* sp. had the highest variations (5.16 ‰ for δ^{13}C and 2.36‰ for δ^{15}N). The group composed by all the other primary producers varied homogeneously (PERMANOVA table S2) with an increase of 0.54 (0.26) ‰ for δ^{13}C and an increase of 2.11 (0.18) ‰ for δ^{15}N.

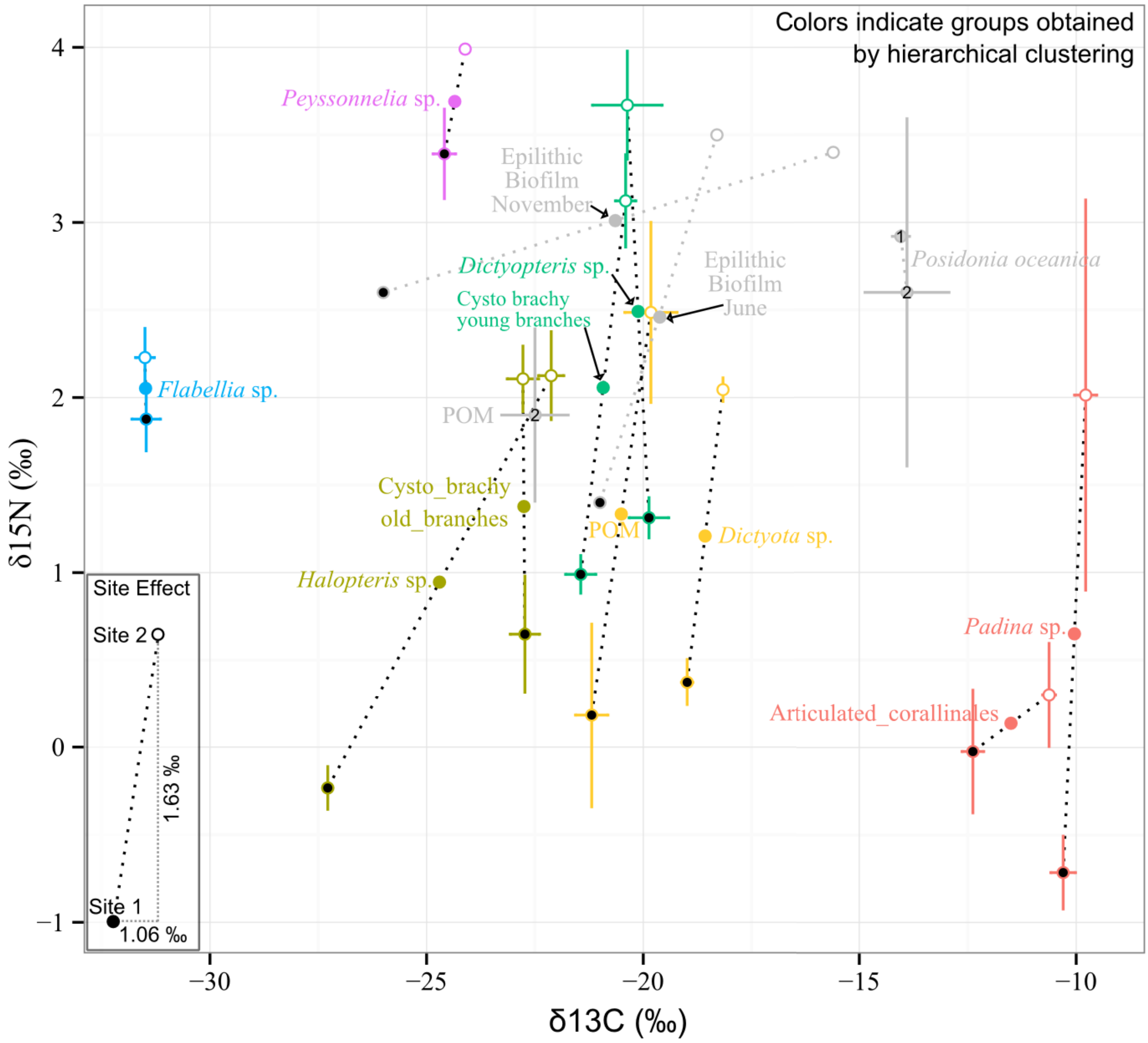


Figure 4: Mean δ^{13}C and δ^{15}N values (± SE) of primary producers, sampled in Site 1 (black filled circle) and in site 2 (white filled circles). Colors indicate groups obtained by hierarchical clustering, carried out on the isotopic values averaged over the 2 sites (the midpoints filled with color). Epilithic biofilm values were measured by Vermulen et al (2011) close to both Site 1 and 2 (see Figure 1). *Posidonia oceanica* values were measured by (1) Pinnegar and Pollunin (2000) and (2) by Lepoint et al (2000), both in sites half-way from site 1 and 2 (see Figure 1). Particulate Organic Matter (POM) marked with a '2' was also measured by Lepoint et al 2000. Cysto_brachy: *Cystoseira brachycarpa.*

3.2.2 Invertebrates

When considering only invertebrates, the matrices of distances between pairs of trophic entities computed for site 1 and 2 were lowly but significantly correlated (Mantel test: r = 0.38, p = 0.012). This indicated that position of trophic entities relatively to each other, were not random from one site to the other. The low value of the correlation coefficient indicated some possible variations in trophic structure of the 2 sites, but PERMANOVAs results (Table S2) suggested this was due to statistical noise (see error bars in Figure 5). Indeed, the terms Trophic Entity and Site were significant, but not the interaction terms Trophic Entity x Site. This absence of statistical evidence for differences between trophic entities in their change across site indicated that isotopic compositions did undergo a global translation from one site to the other site, which indicated similarities in trophic structure of the two sites (Figure 5). Most of the trophic entities had lower $\delta^{13}C$ mean values in site 2 than in site 1 (Table S1). The average difference in $\delta^{13}C$ mean values was 0.70 (0.31) ‰. Most of the trophic entities had higher $\delta^{15}N$ mean values in site 2 than in site 1 (Table S1). The average difference for $\delta^{15}N$ mean values was 0.86 (0.15) ‰.

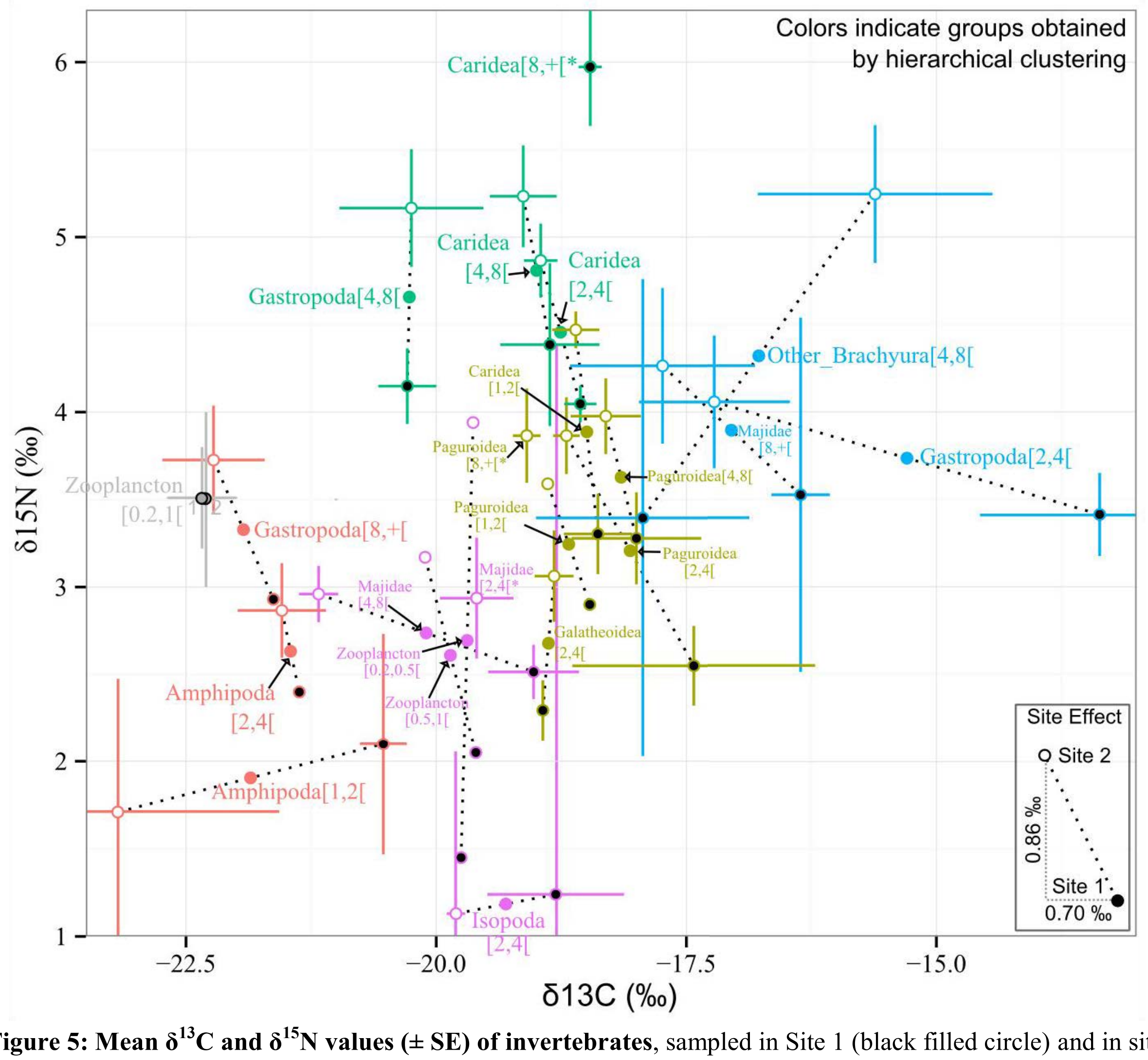


Figure 5: Mean $\delta^{13}C$ and $\delta^{15}N$ values (± SE) of invertebrates, sampled in Site 1 (black filled circle) and in site 2 (white filled circles). Colors indicate groups obtained by hierarchical clustering, carried out on the isotopic values averaged over the 2 sites (the midpoints filled with color). * indicate the trophic entities that were sampled only in one site. Zooplankton [0.2,1[were estimated by (1) Pinnegar and Pollunin (2000) and (2) by Lepoint et al (2000) in sites half-way from site 1 and 2 (see Figure 1)

3.2.3 Fish

When considering only fish, the matrices of distances between pairs of trophic entities computed for site 1 and 2 were correlated (Mantel test: r = 0.47, p = 0.001). This suggested similarities in trophic structure of the two sites. However, PERMANOVAs highlighted that all trophic entities did not homogeneously vary across sites, since the terms Trophic Entity x Site were significant in the PERMANOVAs (Table S2). Differences between trophic entities in their change across sites were in terms of direction and order of magnitude for δ^{13}C values, and were only in terms of order of magnitude for δ^{15}N values (Figure 6 and PERMANOVA and PERMDISP results in Table S2). Hierarchical clustering on differences in isotopic compositions across sites did not reveal clear-cut groups of trophic entities. Each trophic entity had its own site-to-site variations. Nevertheless, 10 out of 13 trophic entities had higher δ^{13}C mean values in site 2 than in site 1, and all trophic entities had higher δ^{15}N mean values in site 2 than in site 1 (Table S1). The average difference in δ^{13}C mean values (SE) was 0.29 (0.11) ‰, and the average difference in δ^{15}N mean values was 0.76 (0.13) ‰. It is worth noting that for the species whose two size-classes were sampled in both sites (*Coris julis*, *Symphodus ocellatus*, *S. roissali* and *Serranus scriba*), site-to-site δ^{15}N-differences were higher for small individuals than for large individuals (Figure 6 and Table S1).

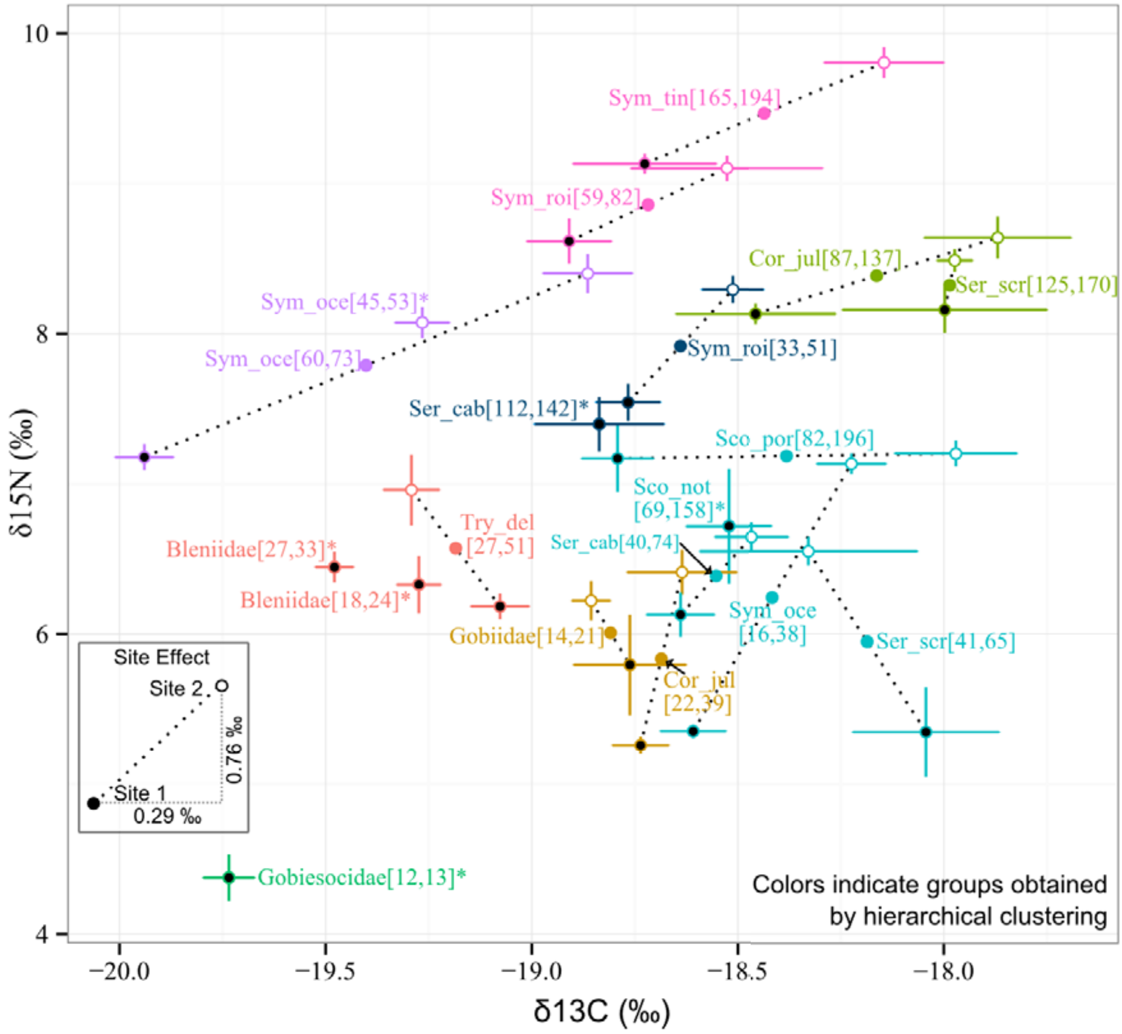


Figure 6: Mean δ^{13}C and δ^{15}N values (± SE) of fish taxa-size class. See legend of Figure 5. Abbreviated labels are the 3 first letters of the genus and the 3 first letters of the species (See Table 1). Numbers within brackets indicate the range of fish body-length (total length in mm).

3.3 Feeding habits of macrocarnivorous fish

3.3.1 Isotopic niches

There was some differences between isotopic niches of *S. cabrilla, S. scriba*, *S. notata* and *S. porcus*, which depended upon the sites (significance of the terms Species x Site in PERMANOVAs of Table S2). Isotopic niches widths were not different (Standard Ellipse Area estimates not distinct in Figure 7, and PERMDISPs not significant in Table S2) so isotopic niches differed only in terms of locations (ellipses coordinates in Figure 7). In both sites, *S. scriba* and *S. porcus* isotopic niches were located differently (pairwise tests in Table S2) and they did almost not overlap (ellipses in Figure 7). Within site 1, *S. scriba* isotopic niche was located differently from the 3 other species whose isotopic niches were not significantly different (pairwise tests in Table S2). Although, their respective isotopic niches overlapped only partially each other, especially *S. notata* isotopic niche that was centered quiet apart from *S. cabrilla* and *S. porcus* isotopic niches (ellipses in Figure 7).

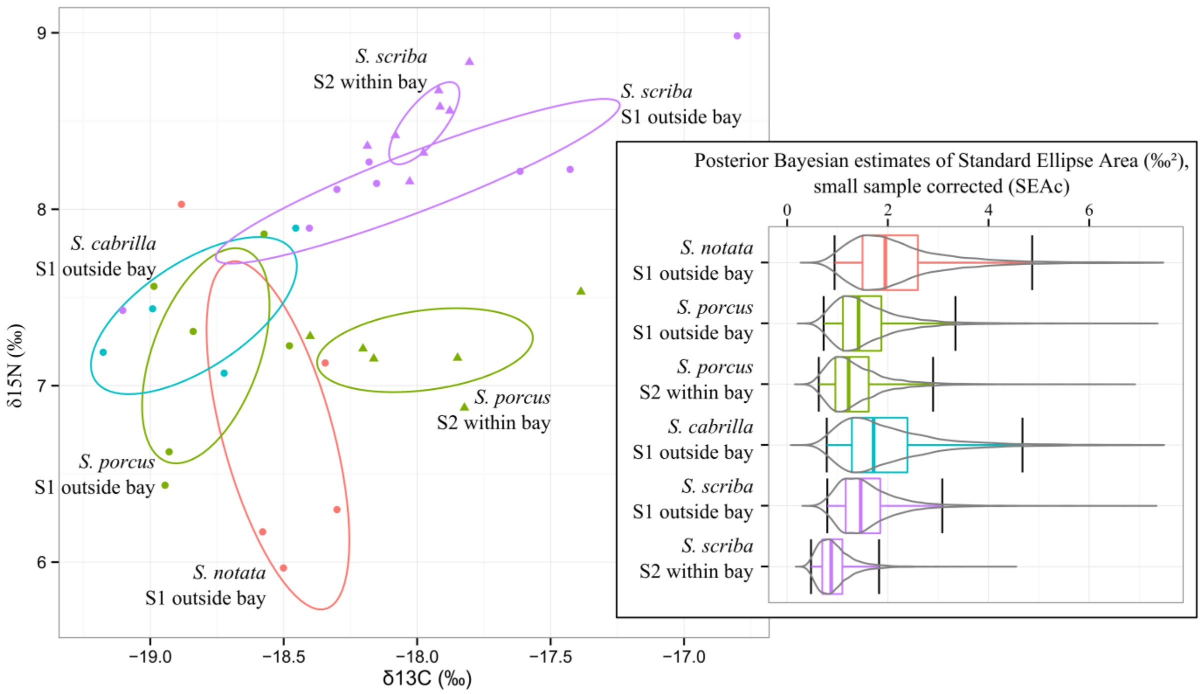


Figure 7: Standard ellipses of macrocarnivorous fish. Left panel, likelihood estimations of the standard ellipses coordinates. Right panel, posterior bayesian estimates of SEAc indicating the isotopic niche widths. Whiskers delimit 95% of the values, which is the Bayesian analogue of a confidence interval.

3.3.2 Stomach contents

The number of non-empty stomachs of *Serranus scriba* was 13 (out of 14 stomachs analyzed) and 11 (out of 16) in Site 1 and Site 2, respectively. No multivariate difference in *S. scriba* food habits was detected between the two sites (PERMANOVA: Pseudo-$F_{1,22}$ = 0.51, p = 0.77; PERMDISP: Pseudo-$F_{1,22}$ = 1.33, p = 0.32). The stomachs of the 4 *S. cabrilla* analyzed were non-empty. Individuals were collected only in Site 1. For *Scorpaena porcus*, 0 stomachs (out of 4) and 15 (out of 22) were non-empty in Site 1 and Site 2, respectively. For

S. notata, the 4 stomachs analyzed were empty. Significant multivariate differences in food habits were detected between *S. scriba*, *S. cabrilla* and *S. porcus*. Differences between species were in term of multivariate locations, not in term of multivariate dispersions (PERMANOVA: Pseudo-$F_{2,40}$ = 2.83, p = 0.004; PERMDISP: Pseudo-$F_{2,40}$ = 3.68, p = 0.11). Food habits of *S. porcus* were significantly different from the 2 others species (pairwise tests, p values < 0.05). Differences between the two *Serranus* species were close to the 0.05 significance threshold (pairwise test, p = 0.09).

S. porcus preyed primarily upon Crustacean (F = 93.3%, mean N (SE) = 77 (8.1) %, mean W (SE) = 83.5 (8.8) %) and secondarily on fish (F = 26.7%, mean N (SE) = 11.9 (6.9) %, mean W (SE) = 14.8 (8.8) %) (Table S3). Crustacean Walker and Swimmer had similar numerical importance (means of N both around 40%) (Figure 8 and Table S3) suggesting that *S. porcus* did not target preferentially one of these two broad functional groups. However, Crustacean Walker had higher weight importance (mean W (SE) = 54.5 (10.9) %) than Crustacean Swimmer (mean W (SE) = 28.7 (9.9) %), suggesting that Crustacean Walker were heavier prey-items that may have higher nutritional importance. Important Crustacean Walker included mostly large Brachyura (Majidae and others, larger than 8 mm). The less important Crustacean Swimmer included mostly medium and large sized Caridea ([4,8[and ≥ 8 mm). In regard to fish, which were secondary prey-items, some individuals were too much digested for allowing more detailed determination. Fish that could be more finely determined were all *Symphodus* spp. juveniles.

S. scriba preyed mainly on Crustacean and fish. Crustacean were slightly more important prey-items (F = 79.2 %, mean N (SE) = 52.9 (7.7) %, mean W (SE) = 53.7 (9.4) %) than were fish (F = 66.7 %, mean N (SE) = 38.9 (7.5) %, mean W (SE) = 41.7 (9.3) %) (Table S3). Crustacean prey-items were mostly Brachyura (Walker), medium to large sized ([4,8[and ≥ 8 mm), whose Galatheoidea larger than 8 mm were the most important (Figure 8 and Table S3). The few Crustacean Swimmer prey-items were only Caridea, mostly larger than 8 mm. In regard to fish prey-items that could be more finely determined, they were all crypto-benthic taxa, mostly *Trypterigion* spp. juveniles and adults (*T. delaisi*). Some Gobiidae and Blenniidae juveniles were sporadically recorded, with low numerical and weight importance.

S. cabrilla preyed primarily on fish (F = 100%, mean N (SE) = 81.2 (12) %, mean W (SE) = 83.7 (21.7) %) and secondarily on Crustacean (F = 50 %, mean N (SE) = 18.8 (12) %, mean W (SE) = 16.3 (7) %) (Table S3). Necto-benthic fish contributed between 55% and 85% and crypto-benthic contributed between 0% and 30%, since mean ponderal importance was around 55% for necto-benthic fish, 0% for crypto-benthic fish, and around 30% for undetermined fish (Figure 8 and Table S3). All fish prey-items that could be more finely determined were juveniles of *Coris julis* (TLs $\in$ [20,40]). The secondary prey-items Crustacean were large (≥ 8 mm) Caridae (Swimmer) and small ([2,4[mm) Isopoda (Walker). It is worth noting that this low diversity in food diet probably reflected the low sampling effort (4 stomach analyzed).

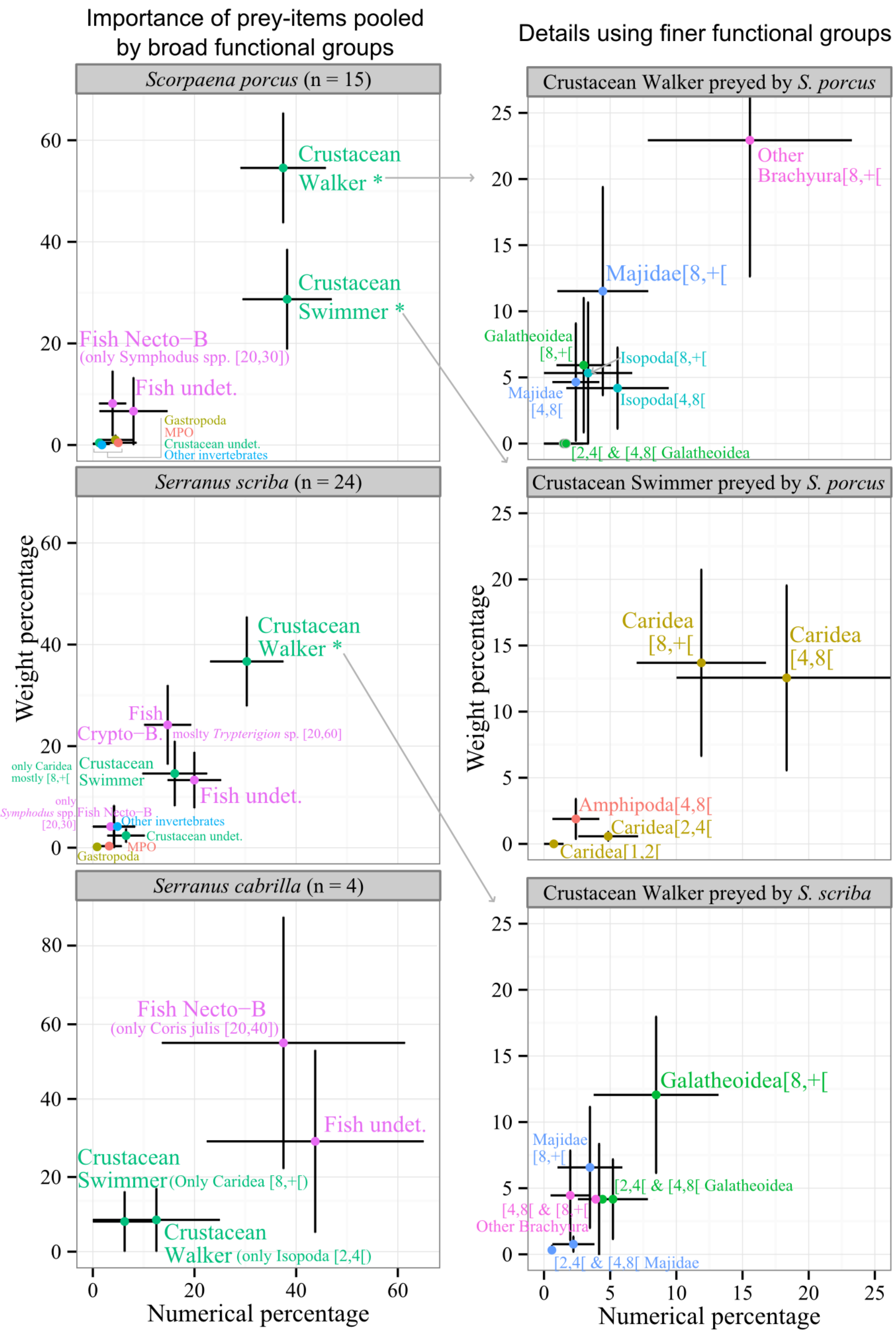


Figure 8: Prey-items' numerical (N) and weight (W) percentage into stomach contents of the 3 macrocarnivorous fish. On the left, prey-items are pooled by broad functional groups (See Tables 1 and S3). When necessary (*), groups are detailed on the right. *S. porcus*: TLs ∈ [105,180], mean TL (SE) = 145.1 (4.5); *S. cabrilla*: TLs ∈ [112,142], mean TL = 125.5 (6.2); *S. scriba*: TLs ∈ [115,217], mean TL = 155.9 (5.4)

3.3.3 Bayesian stable isotope mixing models

SIAR models ran for estimating *S. porcus* dietary proportions in site 1 and site 2, both estimated that Crustacean Walker (Brachyura) were the main prey-items (Lower panel in Figure 9), which is consistent with estimations made from stomach contents. However, in regard to finer functional groups (Middle panel in Figure 9), SIAR models estimated that Galatheoidea [2,4[and Majidae[4,8[were the most contributing Crustacean Walker, contrastingly to stomach contents that suggested as most important prey-items the largest Brachyura (≥ 8 mm). SIAR models' estimations of the contributions of Crustacean Swimmer (Caridea) and necto-benthic fish (juvenile labrids) were less clear cut. Model for site 1 suggested that Caridea contributed almost as much as Brachyura, and that juvenile labrids contributed less (the most likely around 5%, the mode of the distribution). Model for site 2 was underdetermined (bimodal distributions) and two main mutually exclusive scenario were possible (Lower panel in Figure 9, see also Draftmanplots in Figure S4), into which Brachuyra always contributed at around 65 %, while the other varied between scenario 1 and 2 as follow: (1) Caridea contributed to 10% and juvenile labrids to 25%, and (2) Caridea contributed at around 30 % and juvenile labrids at around 5%. This second scenario was closer to the results obtained from the SIAR model for site 1. Assuming that *S. porcus* had the same feeding behavior in both sites, a very low contribution of juvenile labrids (around 5%) into *S. porcus* diet appeared to be the most likely scenario. This SIAR models' estimation of fish importance was lower than stomach contents' estimation, which approached the 15%. Moreover, SIAR models suggested that *Coris julis* juveniles were the most likely to contribute, while only *Symphodus* spp. were found inside stomach contents (along with undetermined prey fish, possibly *C. julis*).

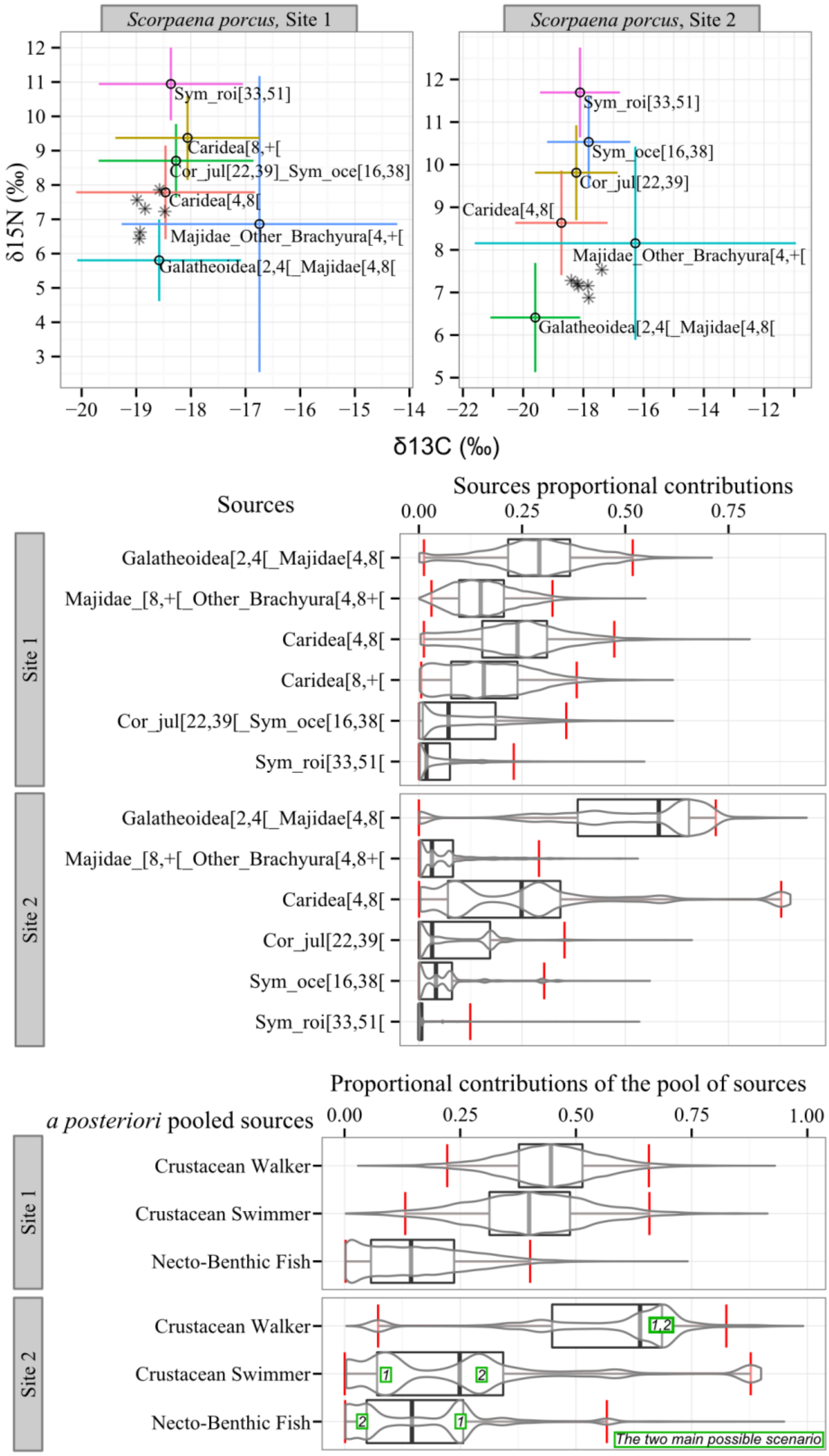


Figure 9: Prey (sources) proportional contributions to diet of *Scorpaena porcus*, estimated by Bayesian isotopic mixing model. Upper panel: colored errorbars indicate δ^{13}C and δ^{15}N mean values (±SD) of the sources after error and fractionation adjustments (δ^{13}C: +1.0 ‰ ± 0.4 ‰ SD; δ^{15}N: +3.4 ‰ ± 1.1 ‰), and asterisk symbols indicate δ^{13}C and δ^{15}N values of each *S. porcus* individual (n = 6 in both sites). **Middle panel:** boxplots and violin plots both summarize the posterior distributions of each source's proportional contribution. **Lower panel:** Posterior distributions of the contributions of sources combined *a posteriori* by functional groups (See Table 1). Green contoured numbers 1 and 2: respective proportional contributions of the two main possible scenarios. For all boxplots, red whiskers delimit 95% of the values.

SIAR models ran for estimating *Serranus scriba* dietary proportions missed a putatively important source, Galatheoidea [8,+[, that was the most important prey-item found in the stomach contents. Galatheoidea [8,+[isotopic compositions could not been assessed since they were not collected despite exhaustive harvesting of macroinvertebrates in 6 sampling area of 1m². Galatheoidea [8,+[isotopic signatures would probably laid within the range of the other Brachyrua, which were the only sources depleted in ^{15}N relatively to the consumers (Upper panel in Figure 10). Therefore, SIAR models had probably distributed the proportional contribution of Galatheoidea [8,+[into the contributions of the other ^{15}N-depleted Brachyura included into the models. From this perspective, SIAR model results about the different Brachyura cannot be reliable, but results about combination of all Brachyura (Crustacean Walker), and about all other sources (those ^{15}N enriched) might be reliable.

In regard to the contributions of sources combined by functional group (Lower panel in Figure 10), their distributions estimated by the model for site 1 were strongly underdetermined, being very wide and multi-modal, due to the 3 sources that were interrelated (Draftmanplot in Figure S4). Two main mutually exclusive scenario were possible (Lower panel in Figure 10): (1) Crustacean Walker (Brachyura) contributed at around 35%, the combined Crustacean Swimmer (Caridea) and necto-benthic fish (juvenile labrids) at around 20%, and the crypto-benthic fish at around 45%, and (2) Crustacean Walker contributed at 45%, the combined Crustacean Swimmer and necto-benthic fish at 45%, and the crypto-benthic fish at around 10%.

SIAR model for site 2 suffered from the same drawback. Two scenarios were likely (Lower panel in Figure 10), into which Crustacean Walker always contributed at around 35-40% and necto-benthic fish around 20-30%, while the other varied between scenario 1 and 2 as follow: (1) Crustacean Swimmer contributed at around 10-15%, and crypto-benthic fish around 20-25%, and (2) Crustacean Swimmer contributed at around 20% and crypto-benthic fish at around 10%.

The respective scenario '2' of models for site 1 and site 2, were comparable and might be accepted as the most likely estimations of *S. scriba* dietary proportions. This most likely SIAR estimation, where Crustacean (Walker around 35-45%, Swimmer around 25-35%) contributed more than fish to *S. scriba* diet, was coherent with stomach content results. However, there was discrepancy between the two methods when discerning fish functional groups. SIAR models suggested that necto-benthic fish contributed (at around 20-30%) more than crypto-benthic fish (around 10%), while stomach contents suggested that the main prey fish of *S. scriba* were crypto-benthic.

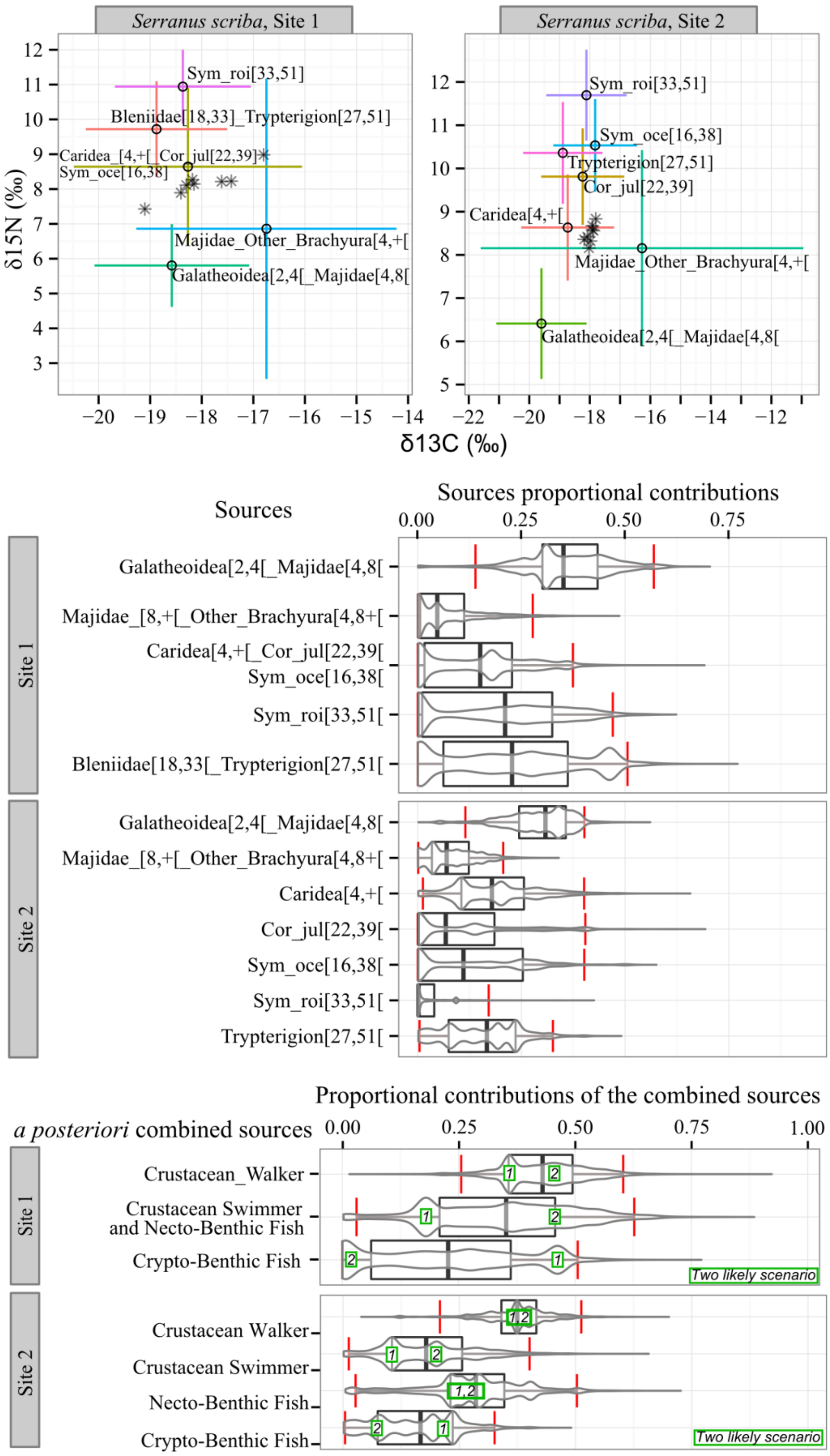


Figure 10: Prey (sources) proportional contributions to diet of *Serranus scriba*, estimated by Bayesian isotopic mixing model. Upper panel: colored errorbars indicate $\delta^{13}C$ and $\delta^{15}N$ mean values (±SD) of the sources after error and fractionation adjustments ($\delta^{13}C$: +1.0 ‰ ± 0.4 ‰ SD; $\delta^{15}N$: +3.4 ‰ ± 1.1 ‰), and asterisk symbols indicate $\delta^{13}C$ and $\delta^{15}N$ values of each *S. scriba* individual (n = 8 in both sites). **Middle panel:** boxplots and violin plots both summarize the posterior distributions of each source's proportional contribution. **Lower panel:** Posterior distributions of the contributions of sources combined *a posteriori* by functional groups (See Table 1). Green contoured numbers 1 and 2: respective proportional contributions of the two main possible scenarios. For all boxplots, red whiskers delimit 95% of the values.

The SIAR model on *S. cabrilla* (only in site 1) was underdetermined. Distributions of every source's proportional contributions had a first mode around 0% and a long tail (Middle panel in Figure 11). This indicated that all sources were interrelated due to a complex system geometry, where high contribution of one source reduced the contribution of the others (Draftman plot in Figure S4). In regard to the distributions of sources combined by functional groups (Lower panel in Figure 11), no clear scenario may be drawn. Most likely estimations of proportional contributions ranged between 30 and 60% for Crustacean Walker, between 20 and 60% for Crustacean Swimmer and necto-benthic fish, and between 0 and 40% for crypto-benthic fish. Stomach contents analyses estimated that necto-benthic fish contributed at around 55% (plus 30% for undetermined fish), and that Crustacean Walker and Swimmer both contributed at around 8%. From this perspective, we could retain the upper bound for Crustacean Swimmer and necto-benthic fish (*i.e.* 60%, possibly 8% for Crustacean Swimmer and 52% for necto-benthic fish), and retain the lower bound of the SIAR estimations for Crustacean Walker (30%), what leads crypto-benthic fish contribution to 10%. These estimations made by SIAR compared to those made by stomach content analyses remained higher for Crustacean Walker (30% in SIAR outputs *vs* 8% in stomach contents), and lower for fish (52% + 10% for necto- + crypto-benthic fish in SIAR outputs, *vs* 55% + 0% + 30% for necto- + crypto-benthic + undetermined fish in stomach contents).

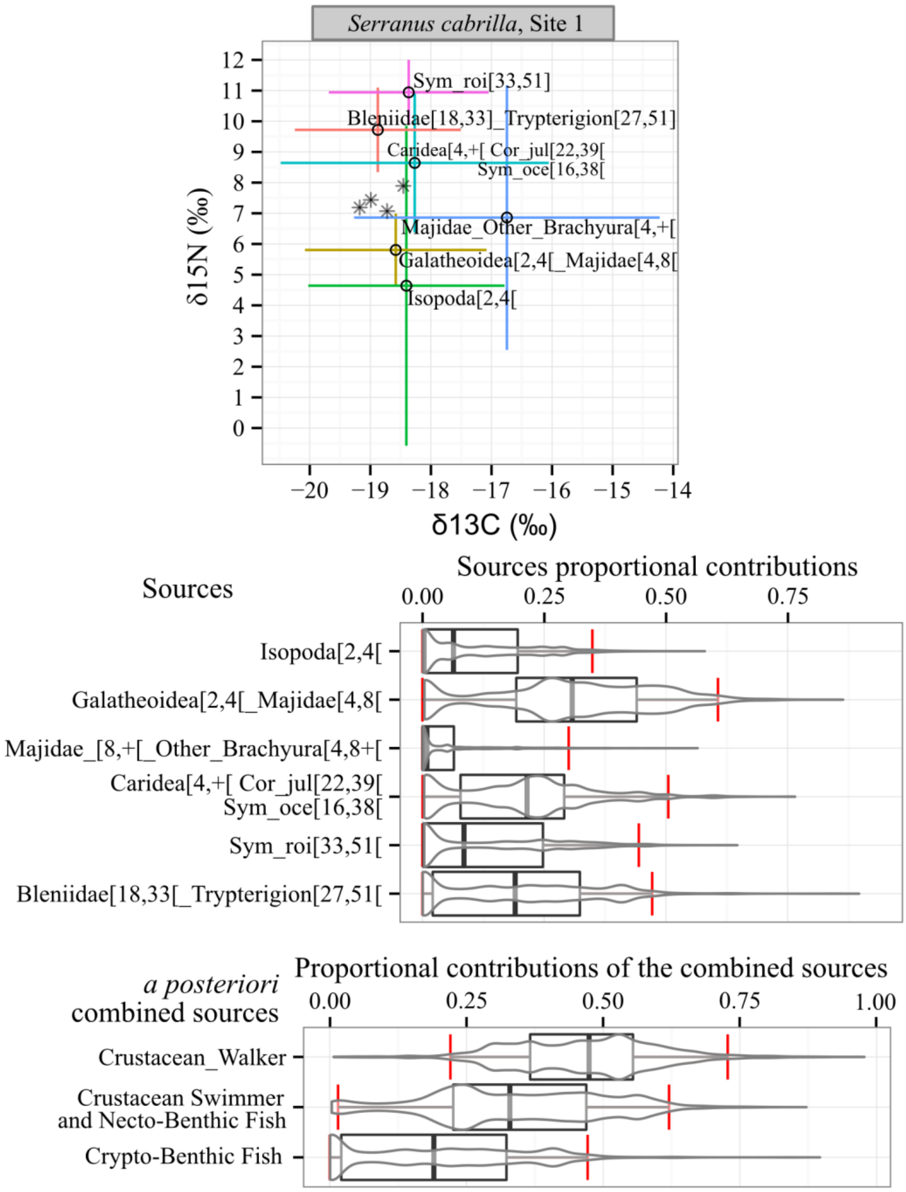


Figure 11: Prey (sources) proportional contributions to diet of *Serranus cabrilla*, estimated by Bayesian isotopic mixing model. Upper panel: colored errorbars indicate $\delta^{13}C$ and $\delta^{15}N$ mean values (±SD) of the sources after error and fractionation adjustments ($\delta^{13}C$: +1.0 ‰ ± 0.4 ‰ SD; $\delta^{15}N$: +3.4 ‰ ± 1.1 ‰), and asterisk symbols indicate $\delta^{13}C$ and $\delta^{15}N$ values of each *S. cabrilla* individual (n = 4 in both sites). **Middle panel:** boxplots and violin plots both summarize the posterior distributions of each source's proportional contribution. **Lower panel:** Posterior distributions of the contributions of sources combined *a posteriori* by functional groups (See Table 1). For all boxplots, red whiskers delimit 95% of the values.

4 Discussion

4.1 Differences between sites in isotopic compositions

Differences in isotopic compositions between sites were globally similar for all trophic entities. Hence, positions into the isotopic space of trophic entities relatively to each other (pairwise distances), were globally similar in both sites. This suggested that trophic structure of *Cystoseira brachycarpa* forest were globally consistent across the two sites investigated.

The global ^{15}N-enrichment in site 2 (within the bay), consistent from primary producers to fishes, was likely due to a shift in δ^{15}N baseline rather than due to changes in trophic levels of organisms. The higher δ^{15}N baseline in site 2 could be related to site-to-site differences in the isotopic compositions of nutrients assimilated by primary producers, due to differential origins of nutrients. The site 1 is open to the high sea while the site 2 is embayed, and this may explain the differential origins of nutrients. Renewal times of water bodies are longer inside the bay, excluding winter periods when there are strong storms. From spring, this reduces inputs inside the bay of new nutrients coming from the sea. Hence, once all new nutrients accumulated during winter are consumed, the primary production inside the bay may rely more on nutrients excreted by faunal organisms (regenerated primary production) and on nutrients released from the sediment (in part terrigenous due to rivers inputs). Comparatively, systems outside the bay receive more new nutrients coming from the sea (eventually through upwelling) and contribution of other nutrients may be lower. Regenerated nutrients and nutrients coming from terrigenous sediment are both ^{15}N-enriched compared to new nutrients coming from the sea (Selmer *et al.* 1993; Pantoja *et al.* 2002). Hence, from spring the embayment of site 2 may increase the relative contribution to primary production of ^{15}N-enriched nutrients, which may increase the δ^{15}N baseline in site 2 and explain the global ^{15}N-enrichment of all trophic entities. An additional effect related to the inputs inside the bay of ^{15}N-enriched nutrients coming from the Calvi sewer and from the Calvi fish farm, cannot be excluded (Vizzini & Mazzola 2004; Vermeulen *et al.* 2011). However, the amounts of discharged anthropogenic nutrients is negligible relatively to the amount of natural nutrients, and therefore their impacts are very localized (Vizzini & Mazzola 2004; Vermeulen *et al.* 2011). The site 2 was hundreds of meters apart from these anthropogenic sources, so their impacts are probably negligible in site 2.

Concerning δ^{13}C values, most primary producers were ^{13}C-enriched in site 2. This is unlikely due to differential origins of dissolved inorganic carbon (mainly dissolved CO^2). This probably resulted from the fact that the site 1 is more shady than site 2, due to its position relative to the high cliffs of the Revellata Cap. Lower sunlight reduce photosynthesis rates in site 2, which in turn affect trophic enrichment factor and reduce δ^{13}C values (Burkhardt *et al.* 1999; Lepoint *et al.* 2003; Stutes *et al.* 2006). Concerning invertebrates, most of trophic entities were ^{13}C-depleted in site 2. This was surprising since the primary producers that we sampled were ^{13}C-enriched in site 2. This might be because invertebrates fed (similarly in both sites) upon other sources, not sampled (*e.g.* detritus, meiofauna), that could have been ^{13}C-depleted in site 2. Or this might be due to differences between sites in feeding habits of invertebrates (*e.g.* due to differential availability in prey-items). Or this might be related to differences between sites in taxonomical compositions of invertebrate assemblages that we could not appreciate by using broad taxonomical group. Concerning fish, most of trophic entities were ^{13}C-enriched in site 2, like primary producers but unlike invertebrates. As for invertebrates, this might be because fish fed (similarly in both sites) upon other sources (especially meiofauna that is preyed by small fish), that could have been ^{13}C-enriched in site 2. Or this might be due to differences between sites in fish feeding habits, possibly due to differential availability in prey-items and/or because fish may have gone forage in other habitats adjacent to the sampled sites: deep corralligenous habitats in site 1 and *Posidonia* meadow in site 2. Despite the fact that site-to-site variations of invertebrates $\delta^{13}C$ compositions were somehow inconsistent with those of primary producers and fish, the patterns of isotopic compositions remained globally consistent across sites.

4.2 The sources of organic matter sustaining the food web

$\delta^{13}C$ values presently measured covered the same ranges than those measured in the Revellata Bay by Lepoint *et al.* (2000), Pinnegar & Polunin (2000) and Dauby (1989). But contrastingly to these studies who found that POM have $\delta^{13}C$ values lower that most of benthic primary producers, the presently-measured $\delta^{13}C$ values did not enable to distinguish the POM from the benthic primary producers, and especially from *Cystoseira brachycarpa* young branches (that grew since Summer). We measured isotopic composition in September. In this season, POM are known to be particularly ^{13}C and ^{15}N enriched, notably due to high photosynthetic rates (long daytime in summer) and to the use of regenerated nutrients. We therefore gathered in Lepoint et al (2000) POM isotopic compositions averaged over the February-October period. Although, this estimation that integrates seasonal variations, was not different from *Cystoseira braycarpa* old branches (that grew since winter) that also integrates seasonal variations. Hence, we never could distinguish POM from *Cystoseira brachycarpa*.

In regard to $\delta^{13}C$ values of POM and *C. brachycarpa* (similarly ranging between -23 and -20.5 ‰ depending on the season) and to $\delta^{13}C$ values of fish (ranging between - 20 ‰ and -18‰), by considering $\delta^{13}C$ trophic enrichment factor (around 1‰ per trophic level), this might be possible that at least one of POM or *C. brachycarpa* contributed importantly as source of organic material sustaining the fish assemblage. Following the same reasoning, some other benthic primary producers might have also contributed (*e.g. Dictyopteris* sp., $\delta^{13}C$ values around -20 ‰) but we can likely exclude the contributions of primary producers that had extreme $\delta^{13}C$ values relatively to the range of fish $\delta^{13}C$ values (extremely low: *Flabellia* sp., *Halopteris* sp., *Peysonnelia* sp.; extremely high: *Posidonia oceanica*, articulated corallinales and *Padina* sp.).

We did not consider detritus in the present study. We possibly missed an important pathway. Indeed, many small benthic invertebrates (but also sea urchins), which are prey of many fishes (Stergiou & Karpouzi 2002), feed upon detritus materials (Lepoint *et al.* 2006). Important sources of detritus include macroalgae, notably the high biomasses of *C. brachycarpa* branches falling twice a year (Hoffmann *et al.* 1992), and possibly *dead* pelagic organisms that sediment (*e.g.* phytoplankton particles, zooplankton carcasses) (Frangoulis *et al.* 2011).

Hence, POM and/or *Cystoseira brachycarpa* and/or some other benthic primary producers were possibly important sources sustaining the fish assemblages, directly as prey of pelagic and benthic primary consumers, and/or indirectly as sources of detritus. The similarities in the estimated isotopic compositions and the absence of estimations for detritus, did not allow to assess the different trophic pathways nor the possible trophic role of *C. brachycarpa* in sustaining fish assemblage. Against the ambiguity associated with similar carbon and nitrogen stable isotopes compositions, the addition of sulfur stable isotope and/or the complementary analysis of fatty acid biomarker can help to assess what are the sources of organic matter sustaining fish assemblage (Park *et al.* 2013). However, identifying fatty acids specific to each primary producer is a laborious preliminary step (Hanson *et al.* 2010).

4.3 Trophic position of organisms in *C. brachycarpa* forests

Increase of $\delta^{15}N$ values across primary producers, invertebrates and fish was consistent with previous studies in this area (e.g.: Jennings *et al.* 1997; Lepoint *et al.* 2000; Pinnegar & Polunin 2000) and the widespread recognition that $\delta^{15}N$ provides a relative measure of trophic level (Post 2002). $\delta^{15}N$ values increased with mean body-size of fish species, and for a given species $\delta^{15}N$ values were higher for larger individuals. This confirmed that larger fish species have usually higher trophic level, and that trophic level increase along fish life-span due to ontogenic diet shift (Deudero *et al.* 2004; Vinagre *et al.* 2011), which may simply consist in preying upon larger individuals of the same prey species.

Isotopic compositions did not allow do distinguish the macro-carnivores *S. cabrilla* and *Scorpaena porcus* while stomach contents revealed some important differences in their feeding habits. Maybe this was related to recent seasonal divergences in their feeding habitats, detectable by stomach contents that are a 'snapshot', but undetectable by isotopic compositions that integrate long-term feeding habits (see below). Although, isotopic compositions did not allow to distinguish mesocarnivorous from macrocarnivorous fish, that have unambiguously different feeding habits (Stergiou & Karpouzi 2002). For instance, *Coris julis* [87,137] and *Serranus scriba* [125,170] had similar isotopic compositions. This was in contradiction with feeding habits estimated by stomach content analyses (see the review Stergiou & Karpouzi 2002 for both species, plus the present study for S. scriba). Stomach contents analyses showed that *C. julis* usually prey on small low trophic level invertebrates and *S. cabrilla* prey on larger invertebrates and small-sized fish. Previous studies that used stable isotopes on Mediterranean infralittoral fish distinguished planktonic feeders such as *Boops boops* and *Spicara* spp. from benthic fish consumers, but they did not clearly distinguish among benthic-feeding fish some fish that have obviously different feeding habits (Jennings *et al.* 1997; Pinnegar & Polunin 2000; Cresson *et al.* 2014), like the present study. This may be due to, among other factors, different preys that have similar isotopic compositions (Pinnegar & Polunin 2000), and/or due to differences in trophic enrichment factors among consumers (Caut *et al.* 2009; Cresson *et al.* 2014). Hence, when studying the trophic position of benthic-feeding fishes, stomach contents analyses seem to provide a better resolution of diet than crude interpretations of stable isotopic ratios, but stomach contents give a snapshot estimations and may miss-estimate importance of prey-items due to differences in prey digestion rates and the amount of non-assimilated material (*e.g.* crustacean exoskeleton)(see 'Introduction' and below).

The combination of stomach contents analyses and stable isotope mixing models could help in estimating fish feeding habits, but we could not apply these approaches to our meso-carnivorous fish, because most of individuals caught had empty-stomach and because isotopic compositions of some putatively important prey-items were lacking, as for instance the benthic and hyper-benthic meiofauna (e.g.: harpacticoids, Bell & Harmelin-Vivien 1983; Khoury 1987; Levi 2004). Concerning the majority of meso-carnivores that had empty stomachs, this was unlikely due to dial rhythm issues, since these fish feed diurnally (Harmelin 1987) and we harvested them in daylight hours. This was more likely due to a too long delay between harvesting and killing. Meso-carnivores were mainly caught alive by scuba and were stored alive in plastic bags until the end of the diving session, when they were killed on the boat (by over-dose). Because one dive lasted in average 2h30, this delay between harvesting and killing was probably too long and fish might have time to digest or regurgitate their food. In regard to lack of isotopic compositions for the putatively important prey meiofauna, this was simply, and unfortunately, because we did not have time. Actually, we sampled within 3 weeks for avoiding temporal biases and also due to logistic constraints. Within this narrow time window, we focused our sampling effort primarily on macrocarnivorous fish and their putative prey (macro-fauna). Indeed, estimating feeding habits of macrocarnivorous fish and assessing if they actually prey on small-sized fish was the most important aim of the present study, with respect to the global aim of the PhD project that was investigating fish prey-predator relationships.

4.4 Feeding habits of macrocarnivorous fish

For *S. scriba*, *S. cabrilla* and *S. porcus*, dietary proportions estimated by stomach content analyses and by SIAR stable isotope mixing models were consistent only when comparing the ranking of the relative importance of crustacean and fish, the two main broad functional groups of prey-items. For *Scorpaeana porcus* and *Serranus scriba*, both methods estimated that crustacean contributed more importantly than fish to their diet, and for *S. cabrilla*, both methods estimated that fish contributed more than crustacean. When considering values rather than rank, or when considering finer functional groups of prey items, there was discrepancy between methods for all 3 macrocarnivores, potentially due to several factors, including (1) the possible use in SIAR models of inaccurate values of trophic enrichment factors, (2) the biases inherent to stomach content analyses such as the inclusion of non-digestible material into ponderal importance estimations and the differential digestion rates among prey-items, and/or (3) the fact that stomach content revealed an instantaneous picture of fish feeding habits while isotopic compositions integrates feeding habits on a longer period into which possible shifts in diet occurred.

We could not input into SIAR models some values of trophic enrichment factors (TEFs) that were specific to the macrocarnivorous species investigated. We preliminarily ran models with the TEFs values estimated by Post *et al.* (2002), and models with TEFs values estimated by using the Caut et. al. methodology (2009). Outputs of models using Post *et al.* values were more consistent with our stomach contents results and were retained. We acknowledge this choice was subjective, but it has to be considered that the only objective method in this respect would be to use TEFs values estimated specifically for the consumer investigated, by using feeding experiment with controlled diet. Nevertheless, the bayesian approach of SIAR models enables to consider the uncertainty about TEFs values (since SIAR consider the distributions of TEFs values, *i.e.* both their mean and SD, Parnell *et al.* 2010) what attenuate biases due to the possible inclusion of inaccurate TEFs.

In regard to possible biases inherent to stomach contents analyses, the putative longer digestion rate of larger prey-items might explain why (1) for *S. porcus*, SIAR models estimated that Galatheoidea [2,4[and Majidae[4,8[were the most contributing crustacean walker while stomach contents suggested the largest Brachyura (≥ 8 mm) as most important prey-items, and also why (2) for *S. scriba*, SIAR models suggested that small-sized necto-benthic fish (only juveniles) contributed more than small- and medium-sized crypto-benthic fish (both juveniles and adults) while stomach contents suggested the opposite.

Possible shift in macrocarnivores feeding habits during the last month preceding sampling could also explain some differences between methods since isotopic compositions would be a mixture of the two diets (before and after diet shift)(Phillips & Eldridge 2006; Guelinckx *et al.* 2007; Xia *et al.* 2013) while stomach contents would revealed only the diet after the shift occurred. Diet shift could be related to recent arrival of macrocarnivores in *C. brachycarpa* forest (habitat shift), but diet shift is more likely due to seasonal changes in availabilities of prey-items. About habitat shift (or just occasional foraging expeditions in adjacent habitats), it cannot be excluded for *Scorpaena* spp. that is known to forage also in *P. oceanica* meadow (Harmelin-Vivien *et al.* 1989), but for *Serranus* species, this is unlikely because they are sedentary and territorial species with small home range (Alos *et al.* 2011), and because they were observed already in May and July in large densities in *C. brachycarpa* forest (Chapter 3). A diet shift along the season is a more likely explanation for all macrocarnivores. An increase along the summer in juvenile fish consumptions might explain why (1) for *S. porcus* SIAR models estimated that fish contribution was around 5% while stomach contents estimated fish contribution around 15%, and why (2) for *S. cabrilla,* SIAR outputs suggested that fish contributed at most at 62% while stomach contents suggested that fish contributed at 84%. This possible increase in fish consumptions along the summer is likely and would be related to the increase in densities of juvenile prey-fish, which settled during the summer (Gobioscidae, Blenniidae, Gobiidae (Beldade *et al.* 2006; Felix-Hackradt *et al.* 2013), *Coris julis*, *Symphodus* spp. (Lejeune 1985; Raventos & Macpherson 2005; Cheminée *et al.* 2013; Felix-Hackradt *et al.* 2013). This phenomenon could be inherent to the temporal dynamic of trophic systems in nursery habitats, as observed in *Posidonia oceanica* meadows, which is another Mediterranean nursery habitat where *Scorpaena* spp. exhibit higher juvenile fish consumption during the summer-autumn period following settlement of many species (Harmelin-Vivien *et al.* 1989).

Due to this likely seasonal shift in macrocarnivore feeding habits once prey juvenile fish were settled in *Cystoseira* forest, we focused only on stomach contents for characterizing foraging strategy of macrocarnivores in this period. The 3 species had low feeding niche overlap and this was probably related to differences in their predation tactic that are mediated by the habitat structure formed by the canopy (see Chapter 4, tank experiments).

S. porcus targeted prey-items distributed both within the canopy and at the canopy - open water interface, by preying primarily on both Walker and Swimmer Crustacean, and secondarily on fish (*Symphodus* sp. juveniles) (Figure 12). Chapter 4 highlighted that *S. porcus* sit-and-wait tactic was not efficient during day-time for preying upon *Symphodus* spp. juveniles that avoided *S. porcus* attack range. At night, *S. porcus* is known to ambush at the interface between canopy and open-water (Harmelin-Vivien *et al.* 1989). Therefore, predation occurred probably during sunset when *Symphodus* spp. juveniles move into the canopy for sleeping there, or during sunrise when they come out from the canopy.

S. cabrilla targeted mainly prey items that are distributed at the canopy - open water interface, by preying primarily on fish (*Coris julis* juveniles) and secondarily on Crustacean (mostly the swimmer Caridae larger than 4 mm) (Figure 12). This indicated that despite the negative effect of canopy on *S. cabrilla* stalk-and-attack strategy (Chapter 4), *S. cabrilla* succeeds to prey efficiently upon necto-benthic juveniles. Contrastingly, the other sit-and-wait predator *S. scriba* targeted mainly prey-items distributed within the canopy, by preying almost equally on Crustacean (mostly the Walker Brachyura larger than 8 mm) and on fish (mostly *Trypterigion* spp.) (Figure 12). These differences between *S. cabrilla* and *S. scriba* in their preferential prey fish could be related to their respective morpho-functional traits. Viladiu *et al.* (1999) highlighted that *S. scriba* has a slower mouth opening movement, resulting in a feeding action of *S. scriba* that takes about 30 ms longer than the one of *S. cabrilla*. This might explain why *S. scriba* target crypto-benthic prey fish that are putatively slower in escaping predator attack, while *S. cabrilla* is able to prey on the faster necto-benthic juveniles. Such feeding-niche partitioning between *S. cabrilla* and *S. scriba* might permit the coexistence of these strongly related species.

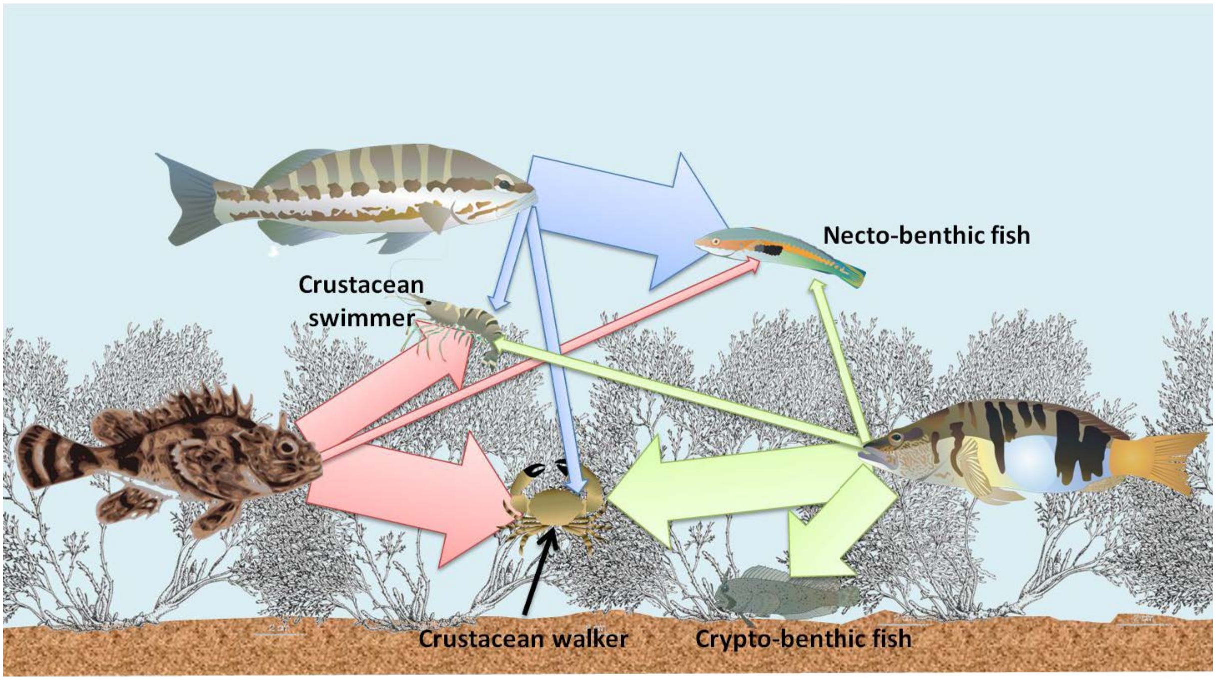
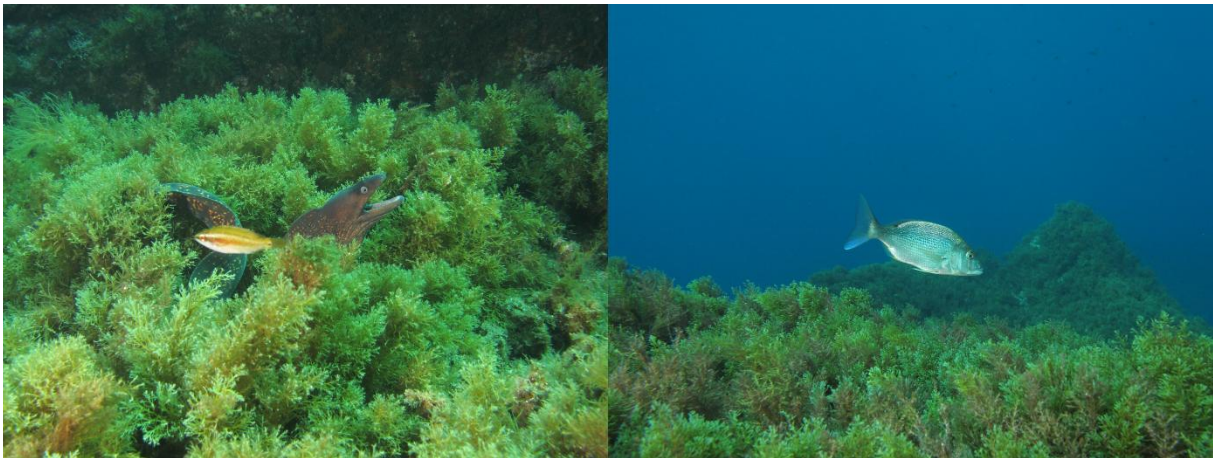


Figure 12. Schematic represetation of macrocarnivorous fish feeding habits assessed by stomach contents analyses. Arrows width indicate the relative contribution of each prey group to feeding habits of *Scorpaena porcus* (red arrows), *Serranus cabrilla* (blue arrows) and *Serranus scriba* (green arrows).

For *S. notata*, unfortunately the 4 collected individuals had empty-stomach. We therefore had no data to input as prior information into the (Bayesian) isotope mixing model. This led model-outputs to be completely underdetermined, *i.e.* posterior estimations of every sources had the same flat distribution. These uninformative results were therefore not reported. Nevertheless, we gleaned some clues from standard ellipses. They suggested that *S. notata* isotopic niche was different from the 3 other macrocarnivores, although isotopic compositions were not significantly different according to PERMANOVAs, probably due to low replications and low power of this test (Warton *et al.* 2012). Harmelin-Vivien *et al.* (1989) showed that *S. notata* feeding habits differed from *S. porcus* in *P. oceanica* meadow. Since the presently estimated feeding habits of *S. porcus* inhabiting *C. brachycarpa* forest corroborate with those of *S. porcus* inhabiting *P. oceanica* meadow (Harmelin-Vivien *et al.* 1989), this might be the case also for *S. notata*. Assuming this strong assumption, it might be speculated that *S. notata* don't prey importantly on fish in *C. brachycarpa* forest, because *S. notata* prey in *P. oceanica* meadow primarily upon Caridae, secondarily on brachyrans and rarely on fish.

Other macrocarnivorous or strictly piscivorous fish are very likely present in *Cystoseira brachycarpa* forest, such as the mainly nocturnal *Conger conger, Murena helena* and *Phycis phycis,* and the transient *Dentex dentex* (personal observations and Photos panel 1). Their nocturnal or transient behavior did not allow to estimate their densities in chapter 3, but they are certainly lower than those of the 3 macrocarnivores presently investigated, as observed for other habitats as *P oceanica* meadows (Bell & Harmelin-Vivien 1982). These high-level predators feed principally on larger prey-items and occasionally or rarely on small-sized fish (Cau & Manconi 1984; Göthel 1992; Morales-Nin & Moranta 1997; Cresson *et al.* 2014). Hence, the most important predator of small sized fish in *Cystoseira brachycarpa* forest are probably the 3 macrocarnivores presently investigated, and more particularly the two *Serranus* spp..



Photos panel 1. Two high level predators observed in *Cystoseira brachycarpa* forests, at the Revellata Bay. Left: *Murena helena*; Right: *Dentex dentex*. Photo credit: Arnaud ABADIE.

From the perspective of crypto-and necto-benthic prey-fish, the present results and those of chapter 4 (tank experiments) suggest that two mechanisms related to predation contribute to their higher densities in *Cystoseira brachycarpa* forest compared to the less structurally complex habitat Turf and Barren (Chapter 3): (1) the *Cystoseira* canopy provide more shelter against predation (Chapter 4), and (2) the *Cystoseira* canopy hosts more crustacean (Chemello & Milazzo 2002; Gozler *et al.* 2010; Pitacco *et al.* 2014) that are also prey items of the 3 macrocarnivores (present chapter), what probably reduce predation pressure undergo by prey-fish. This latter mechanism stresses the importance of carrying out field-based experiments for comparing between habitats predation mortality of small-sized fish, as already discussed in Chapter 4. Moreover, the trophic role of crypto-benthic fish (at least for *S. scriba*) stresses the need to assess reliably crypto-benthic fish densities when characterizing fish assemblage structures, what may be accomplished by using enclosed anesthetic station (Chapter 3).

5 Conclusion

Isotopic compositions were different between the two sites probably due to the embayment of sites 2 and the more shady location of site 1. Nevertheless, trophic organization were similar in both sites, suggesting that the two system had similar trophic functioning. POM and/or *Cystoseira brachycarpa* and/or some other benthic primary producers were possibly important sources sustaining the fish assemblages, directly as prey of pelagic and benthic primary consumers, and/or indirectly as sources of detritus. Although, isotopic compositions did not allow to distinguish the different pathways and we could not assess importance of *Cystoseira brachycarpa* as source of organic matter for the system. The 3 macrocarnivorous fish investigated preyed on both crustacean and fish, with just partial overlap in their feeding niche. Prey-fish contribution to macrocarnivores' diets probably increased during the summer as a consequence of increased juvenile fish densities following settlement. *Serranus cabrilla* and *S. scriba* were the most important predator of necto-benthic fish (juveniles), and crypto-benthic fish (juveniles and adults), respectively. The fact that the macrocarnivores preyed also on crustacean suggested that *Cystoseira brachycarpa* may indirectly reduce predation mortality of small-sized fish by hosting crustacean in high densities.

Supplementary information available at the end of the chapter:

- Table S1: Isotopic compositions estimated in site 1 and 2, and differences between sites in their mean value
- Table S2: Results of PERMANOVAs and PERMDISP on isotopic compositions
- Table S3: Detailed diet proportions of the 3 macrocarnivorous fish
- Figure S4: Draftsman’s plots of posterior source contributions

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7 Supplementary Information

Table S1: Isotopic compositions (mean ± SE) estimated in site 1 and 2, and differences between sites in their mean value. n, number of replicate per site; see Table 1 for the meanings of Loc., Beh., and diet.

Table S1 Part 1, primary producers

	n		$\delta^{13}C$			$\delta^{15}N$		
			S1	S2	S2 – S1 means	S1	S2	S2 – S1 means
Functioal group	**S1**	**S2**	**mean ± SE**	**mean ± SE**	**mean ± SE**	**mean ± SE**	**mean ± SE**	**mean ± SE**
Particulate organic matter	8	8	-21.19 ± 0.37	-19.82 ± 0.6	1.37 ± 0.71	0.18 ± 0.53	2.49 ± 0.52	2.3 ± 0.75
Articulated corallinales	6	6	-12.38 ± 0.25	-10.62 ± 0.15	1.76 ± 0.29	-0.02 ± 0.36	0.3 ± 0.3	0.32 ± 0.47
Cystoseira brachycarpa (old branches)	6	6	-22.73 ± 0.34	-22.78 ± 0.36	-0.05 ± 0.5	0.65 ± 0.34	2.11 ± 0.2	1.46 ± 0.39
Cystoseira brachycarpa (young branches)	6	6	-21.44 ± 0.35	-20.41 ± 0.24	1.04 ± 0.42	0.99 ± 0.12	3.12 ± 0.27	2.13 ± 0.3
Dictyopteris sp.	6	5	-19.87 ± 0.46	-20.37 ± 0.8	-0.5 ± 0.92	1.31 ± 0.12	3.67 ± 0.32	2.36 ± 0.34
Dictyota sp.	6	6	-18.99 ± 0.13	-18.16 ± 0.04	0.83 ± 0.14	0.37 ± 0.14	2.04 ± 0.08	1.67 ± 0.16
Flabellia sp.	6	6	-31.47 ± 0.33	-31.5 ± 0.22	-0.03 ± 0.4	1.88 ± 0.19	2.23 ± 0.17	0.35 ± 0.26
Halopteris sp.	6	6	-27.28 ± 0.11	-22.12 ± 0.29	5.16 ± 0.31	-0.23 ± 0.13	2.12 ± 0.26	2.36 ± 0.29
Padina sp.	6	6	-10.3 ± 0.28	-9.78 ± 0.26	0.52 ± 0.38	-0.72 ± 0.22	2.01 ± 1.12	2.73 ± 1.14
Peyssonnelia sp.	6	1	-24.59 ± 0.26	-24.11	0.48	3.39 ± 0.26	3.99	0.6
min			-31.47	-31.5	-0.5	-0.72	0.3	0.32
max			-10.3	-9.78	5.16	3.39	3.99	2.73
mean			-21.02 ± 2.00	-19.97 ± 1.99	1.06 ± 0.50	0.78 ± 0.38	2.41 ± 0.33	1.63 ± 0.29

Table S1 Part2, Invertebrates

					$\delta^{13}C$									$\delta^{15}N$								
	Body size in mm		**n**		**S1**			**S2**			**S2 – S1 means**			**S1**			**S2**			**S2 – S1 means**		
Functional group		**Loc..**	**S1**	**S2**	**mean**	**±**	**SE**	**mean**	**±**	**SE**	**mean**	**±**	**SE**	**mean**	**±**	**SE**	**mean**	**±**	**SE**	**mean**	**±**	**SE**
Zooplancton	[0.2,0.5[		1	1	-19.75			-19.63			0.12			1.45			3.94			2.49		
Zooplancton	[0.5,1[		1	1	-19.6			-20.11			-0.51			2.05			3.17			1.12		
Gastropoda	[2,4[	W	6	4	-13.37	±	1.29	-17.22	±	0.76	-3.85	±	1.5	3.41	±	0.24	4.06	±	0.38	0.64	±	0.45
Gastropoda	[4,8[	W	6	5	-20.29	±	0.29	-20.25	±	0.72	0.04	±	0.78	4.15	±	0.22	5.17	±	0.34	1.02	±	0.4
Gastropoda	[8,+[	W	1	5	-21.63			-22.22	±	0.51	-0.6			2.93			3.73	±	0.31	0.8		
Amphipoda	[1,2[	CS	3	2	-20.53	±	0.23	-23.18	±	1.9	-2.65	±	1.91	2.1	±	0.63	1.71	±	0.79	-0.39	±	1.01
Amphipoda	[2,4[	CS	1	5	-21.37			-21.54	±	0.44	-0.17			2.4			2.87	±	0.27	0.47		
Caridea	[1,2[	CS	3	4	-18.38	±	0.34	-18.61	±	0.24	-0.22	±	0.41	3.3	±	0.23	4.47	±	0.1	1.17	±	0.25
Caridea	[2,4[	CS	6	7	-18.56	±	0.16	-18.96	±	0.17	-0.4	±	0.23	4.05	±	0.1	4.87	±	0.21	0.82	±	0.24
Caridea	[4,8[	CS	4	6	-18.86	±	0.5	-19.13	±	0.33	-0.27	±	0.6	4.38	±	0.46	5.23	±	0.29	0.85	±	0.55
Caridea	[8,+[	CS	4	0	-18.46	±	0.12	-			-			5.97	±	0.36	-			-		
Isopoda	[2,4[	CW	2	3	-18.81	±	0.68	-19.8	±	0.09	-1	±	0.69	1.24	±	3.62	1.13	±	0.94	-0.11	±	3.74
Galatheoidea	[2,4[	CW	6	4	-18.93	±	0.04	-18.82	±	0.19	0.11	±	0.2	2.29	±	0.17	3.06	±	0.26	0.77	±	0.31
Majidae	[2,4[	CW	0	3	-			-19.6		0.37	-			-			2.94	±	0.35	-		
Majidae	[4,8[	CW	2	3	-19.03	±	0.45	-21.18	±	0.2	-2.15	±	0.5	2.51	±	0.16	2.96	±	0.16	0.45	±	0.22
Majidae	[8,+[	CW	5	5	-16.36	±	0.29	-17.74	±	0.93	-1.38	±	0.97	3.53	±	1.01	4.26	±	0.44	0.74	±	1.11
Paguroidea	[1,2[	CW	1	1	-18.47			-18.89			-0.42			2.9			3.59			0.69		
Paguroidea	[2,4[	CW	4	6	-17.43	±	1.22	-18.7	±	0.13	-1.27	±	1.22	2.55	±	0.23	3.86	±	0.22	1.31	±	0.32
Paguroidea	[4,8[	CW	6	6	-18	±	0.65	-18.31	±	0.35	-0.31	±	0.74	3.28	±	0.26	3.98	±	0.22	0.7	±	0.34
Paguroidea	[8,+[	CW	0	6	-			-19.1	±	0.14	-			-			3.87	±	0.27	-		
Other Brachyura	[4,8[	CW	2	7	-17.94	±	1.07	-15.61	±	1.17	2.32	±	1.59	3.39	±	1.36	5.25	±	0.39	1.85	±	1.42
				min	-21.63			-23.18			-3.85			1.24			1.13			-0.39		
				max	-13.37			-15.61			2.32			5.97			5.25			2.49		
				mean	-18.72	±	0.42	-19.43	±	0.39	-0.70	±	0.31	3.05	±	0.26	3.71	±	0.24	0.86	±	0.15

Table S1 Part 3, fish

						$\delta^{13}C$			$\delta^{15}N$		
	Total length			n		S1	S2	S2 – S1 means	S1	S2	S2 – S1 means
Taxa	in mm	beh.	Diet	S1	S2	mean ± SE	mean ± SE	mean ± SE	mean ± SE	mean ± SE	mean ± SE
Bleniidae	[18,24]	CB	Om	6	0	-19.27 ± 0.05	-	-	6.33 ± 0.19	-	-
Bleniidae	[27,33]	CB	Om	6	0	-19.48 ± 0.05	-	-	6.45 ± 0.1	-	-
Coris julis	[22,39]	NB*	Me	11	11	-18.74 ± 0.07	-18.64 ± 0.13	0.1 ± 0.15	5.26 ± 0.06	6.41 ± 0.15	1.15 ± 0.16
Coris julis	[87,137]	NB	Me	6	6	-18.46 ± 0.19	-17.87 ± 0.18	0.59 ± 0.26	8.13 ± 0.07	8.64 ± 0.14	0.51 ± 0.16
Gobiesocidae	[12,13]	CB	Me	6	0	-19.73 ± 0.06	-	-	4.38 ± 0.15	-	-
Gobiidae	[14,21]	CB	Me	8	9	-18.76 ± 0.14	-18.86 ± 0.05	-0.09 ± 0.14	5.8 ± 0.33	6.22 ± 0.13	0.43 ± 0.36
Scorpaena notata	[69,158]	CB	Ma	5	0	-18.52 ± 0.1	-	-	6.72 ± 0.38	-	-
Scorpaena porcus	[82,196]	CB	Ma	6	6	-18.79 ± 0.09	-17.97 ± 0.15	0.82 ± 0.17	7.17 ± 0.22	7.2 ± 0.09	0.03 ± 0.24
Serranus cabrilla	[40,74]	NB*	Ma	11	11	-18.64 ± 0.08	-18.47 ± 0.09	0.17 ± 0.12	6.13 ± 0.15	6.65 ± 0.1	0.52 ± 0.18
Serranus cabrilla	[112,142]	NB	Ma	4	0	-18.84 ± 0.16	-	-	7.4 ± 0.18	-	-
Serranus scriba	[41,65]	NB*	Ma	2	5	-18.04 ± 0.18	-18.33 ± 0.26	-0.29 ± 0.32	5.35 ± 0.3	6.55 ± 0.1	1.2 ± 0.31
Serranus scriba	[125,170]	NB	Ma	8	8	-18 ± 0.25	-17.97 ± 0.04	0.02 ± 0.25	8.16 ± 0.15	8.49 ± 0.08	0.33 ± 0.17
Symphodus ocellatus	[16,38]	NB*	Me	18	31	-18.61 ± 0.08	-18.22 ± 0.08	0.38 ± 0.12	5.35 ± 0.05	7.13 ± 0.07	1.78 ± 0.08
Symphodus ocellatus	[45,53]	NB	Me	0	15	-	-19.27 ± 0.07	-	-	8.07 ± 0.1	-
Symphodus ocellatus	[60,73]	NB	Me	14	7	-19.94 ± 0.07	-18.86 ± 0.11	1.08 ± 0.13	7.18 ± 0.09	8.4 ± 0.13	1.22 ± 0.16
Symphodus roissali	[33,51]	NB*	Me	8	13	-18.77 ± 0.08	-18.51 ± 0.08	0.25 ± 0.11	7.54 ± 0.12	8.29 ± 0.09	0.75 ± 0.15
Symphodus roissali	[59,82]	NB	Me	8	6	-18.91 ± 0.1	-18.53 ± 0.23	0.38 ± 0.25	8.62 ± 0.15	9.1 ± 0.09	0.49 ± 0.17
Symphodus tinca	[165,194]	NB	Me	6	6	-18.73 ± 0.17	-18.14 ± 0.14	0.58 ± 0.23	9.13 ± 0.07	9.81 ± 0.1	0.67 ± 0.12
Trypterigion delaisi	[27,51]	CB	Me	7	7	-19.08 ± 0.07	-19.29 ± 0.07	-0.21 ± 0.1	6.18 ± 0.09	6.96 ± 0.24	0.78 ± 0.25
					min	-19.94	-19.29	-0.29	4.38	6.22	0.03
					max	-18	-17.87	1.08	9.13	9.81	1.78
					mean	-18.85 ± 0.12	-18.50 ± 0.12	0.29 ± 0.11	6.74 ± 0.30	7.71 ± 0.30	0.76 ± 0.13

Table S2: Results of PERMANOVAs and PERMDISP, comparing isotopic compositions between Trophic Entities (TE) and Sites (Si). ^{ns} not significant; ° $p < 0.1$; * $p < 0.05$; ** $p < 0.01$. *** $p < 0.001$.

Primary producers

		$\delta^{13}C$ & $\delta^{15}N$			$\delta^{13}C$			$\delta^{15}N$		
Source	**df**	**SS**	**F**		**SS**	**F**		**SS**	**F**	
All primary producers										
TE	9	139.74	**36.59**	***	110.27	**576.47**	***	29.48	**8.13**	***
Si	1	27.82	**65.57**	***	0.73	**34.38**	***	27.09	**67.21**	***
TE x Si	9	10.23	**2.68**	*	1.81	**9.47**	***	8.42	**2.32**	*
Res	98	41.58			2.08			39.50		
PERMDISP		TE x Si : $F_{19,98}$=**6.78 *****			TE x Si : $F_{19,98}$ = **2.99 ***			TE x Si : $F_{19,98}$ **= 6.40 *****		
Subset composed by articulated corallinales, *Flabellia* sp. and *Peysonnelia* sp.										
TE	2	49.13	**120.80**	***	29.47	**3257.30**	***	19.66	**49.45**	***
Si	1	0.44	2.19	ns	0.03	**7.16**	*	0.41	2.07	ns
TE x Si	2	0.08	0.21	ns	0.06	**6.58**	**	0.02	0.06	ns
Res	25	5.08			0.11			4.97		
PERMDISP		TE : $F_{2,28}$ = 0.73 ^{ns}			TE x Si : $F_{5,25}$ = 1.99 ^{ns}			TE : $F_{2,28}$ = 0.55 ^{ns}		
Subset composed by *Halopteris* sp.										
Si	1	20.17	**109.97**	**	10.61	**272.45**	**	9.56	**66.16**	**
Res	10	1.83			0.39			1.44		
PERMDISP		Si : $F_{1,10}$ = **5.50 ***			Si : $F_{1,10}$ = **4.31 ***			Si : $F_{1,10}$ = 2.98 ^{ns}		
Subset composed by all other primary producers										
TE	5	79.16	**28.45**	***	69.53	**237.57**	***	9.62	**3.87**	**
Si	1	32.19	**57.86**	***	0.30	**5.09**	*	31.89	**64.06**	***
TE x Si	5	1.72	0.62	ns	0.43	1.48	ns	1.29	0.52	ns
Res	63	35.05			3.69			31.36		
PERMDISP		TE : $F_{5,69}$ = 2.22 ^{ns} Si : $F_{1,73}$ = 0.59 ^{ns}			TE : $F_{5,69}$ = **6.88 ***** Si : $F_{1,73}$ = **0.03 ***			TE : $F_{5,69}$ = 1.73 ^{ns} Si : $F_{1,73}$ = 3.02 °		

Invertebrates

		$\delta^{13}C$ & $\delta^{15}N$			$\delta^{13}C$			$\delta^{15}N$		
Source	**df**	**SS**	**F**		**SS**	**F**		**SS**	**F**	
TE	17	115.92	**7.36**	***	59.23	**8.84**	***	56.69	**6.26**	***
Si	1	10.50	**11.33**	***	1.92	**4.88**	*	8.58	**16.10**	***
TE x Si	17	13.66	0.87	ns	9.68	1.44	ns	3.98	0.44	ns
Res	99	91.75			39.02			52.73		
PERMDISP		TE : $F_{17,117}$ = **5.50 ***** Si : $F_{1,133}$ = 0.09 ^{ns}			TE : $F_{17,117}$ = **4.34 **** Si : $F_{1,133}$ = 0.30 ^{ns}			TE : $F_{17,217}$ = **5.11 ***** Si : $F_{1,133}$ < 0.01 ^{ns}		

Table S2 (continued):

All fish

		$\delta^{13}C$ & $\delta^{15}N$			$\delta^{13}C$			$\delta^{15}N$		
Source	**df**	**SS**	**F**		**SS**	**F**		**SS**	**F**	
TE	12	276.07	**46.38**	***	29.71	**18.51**	***	287.14	**158.99**	***
Si	1	29.27	**59.00**	***	3.96	**29.57**	***	26.78	**177.92**	***
TE x Si	12	31.29	**5.26**	***	6.90	**4.30**	***	16.48	**9.13**	***
Res	213	105.65			28.49			32.06		
PERMDISP		TE x Si : $F_{25,213}$ = **2.10 ***			TE x Si : $F_{25,213}$ = **2.43 ****			TE x Si : $F_{25,213}$ = 1.91 °		

Only the 4 macrocarnivorous fish species

		$\delta^{13}C$ & $\delta^{15}N$			$\delta^{13}C$			$\delta^{15}N$		
Source	**df**	**SS**	**F**		**SS**	**F**		**SS**	**F**	
TE	3	27.71	**9.90**	***	2.12	**3.7**	*	7.11	**19.78**	***
Si	1	4.78	**5.12**	*	4.41	**7.69**	**	0.37	1.04	ns
TE x Si	1	4.17	**4.47**	*	3.92	**6.83**	*	0.25	0.70	ns
Res	31	28.92			0.57			0.36		
PERMDISP		TE x Si : $F_{5,31}$ = 2.37 ns			TE x Si : $F_{5,31}$ = **3.83 ***			TE x Si : $F_{3,33}$= **3.48 ***		
Pairwise tests		Si1: Snot = Spor = Scab ≠ Sscr Si2: Spor ≠ Sscr			Si1: Snot = Spor = Scab ≠ Sscr Si2: Spor ≠ Sscr			Snot = Spor = Scab ≠ Sscr		

Snot: *Scorpaena notata*; Spor: *S. porcus*; Scab: *Serranus cabrilla*; Sscr: *S. scriba*
Post-hoc comparisons among pairs of species: Si1, within Site 1 ; Si2, within Site 2.

Table S3: Detailed diet proportions of the 3 macrocarnivorous fish. n: number of non-empty stomachs considered; F: prey-item frequency; N: mean (SE) numerical importance; W: mean (SE) ponderal importance. In the upper part of the table, data were reported once pooled by very broad functional groups (FG) of prey-items; in the intermediate part, pooled by broad FG, in the lower part: pooled by fine FG. '*' were prey-items whose very-broad and broad FG pooling were similar. '**' were prey-items whose broad and fine FG pooling were similar.

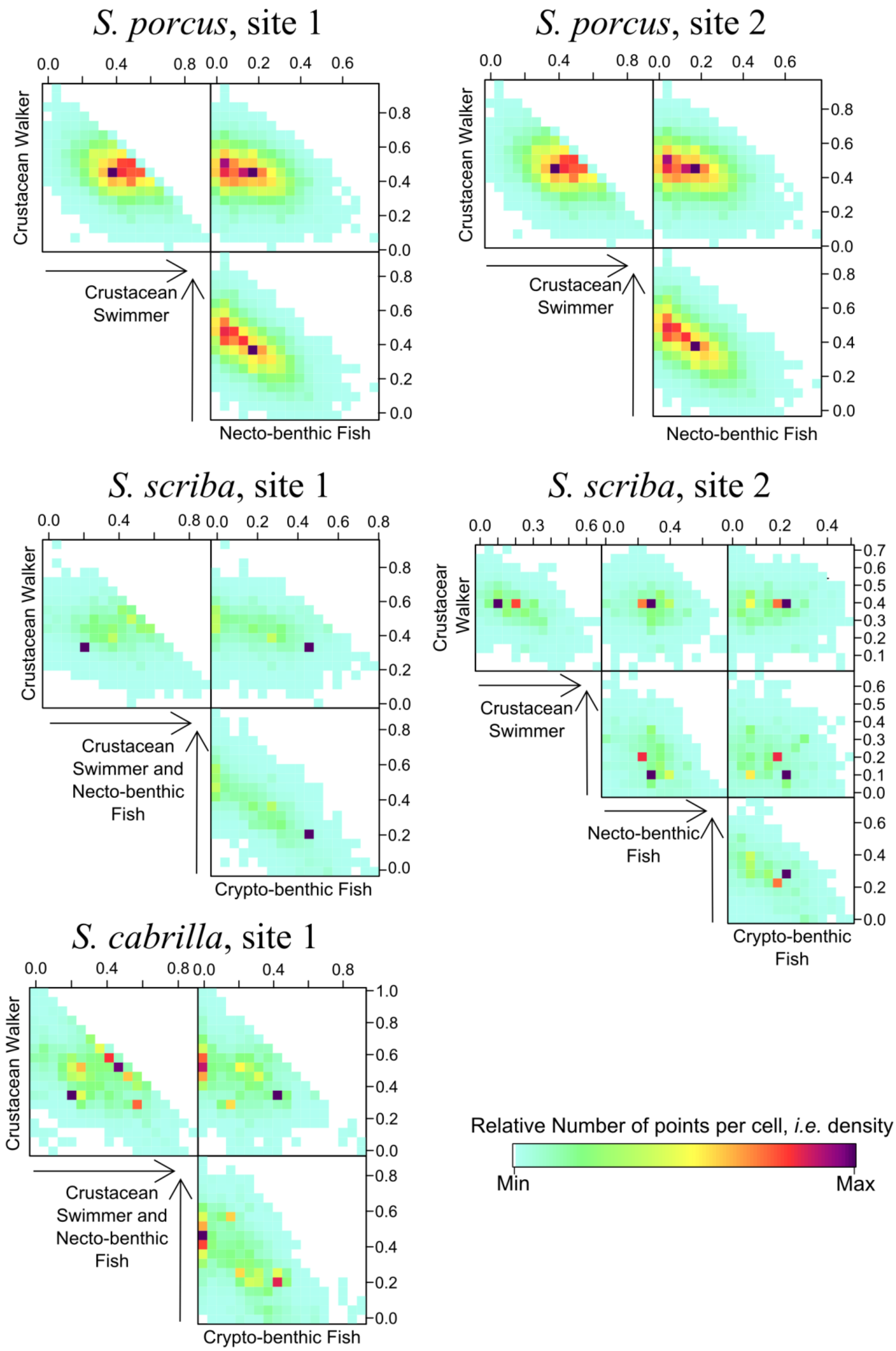
(Very) broad Functional G.	Fine Functional G.	*S. porcus* (n = 15) F	*S. porcus* N mean (SE)	*S. porcus* W mean (SE)	*S. cabrilla* (n = 4) F	*S. cabrilla* N mean (SE)	*S. cabrilla* W mean (SE)	*S. scriba* (n = 24) F	*S. scriba* N mean (SE)	*S. scriba* W mean (SE)
MPO *	Total	13.3	5 (3.6)	0.4 (0.4)	-	-	-	8.3	3.2 (2.5)	0.3 (0.3)
Gastropoda *	Total	13.3	4.4 (3.4)	1 (1)	-	-	-	4.2	0.8 (0.8)	0.2 (0.2)
Crustacean	Total	93.3	77 (8.1)	83.5 (8.8)	50	18.8 (12)	16.3 (7)	79.2	52.9 (7.7)	53.7 (9.4)
Other invertebrates *	Total	6.7	1.7 (1.7)	0.2 (0.2)	-	-	-	4.2	4.2 (4.2)	4.2 (4.2)
Fish	Total	26.7	11.9 (6.9)	14.8 (8.8)	100	81.2 (12)	83.7 (21.7)	66.7	38.9 (7.5)	41.7 (9.3)
Crustacean undet.**	Total	6.7	1.3 (1.3)	0.3 (0.3)	-	-	-	12.5	6.5 (3.7)	2.4 (1.4)
Crustacean Walker	Total	80	37.4 (8.4)	54.5 (10.9)	25	12.5 (12.5)	8.3 (8.3)	54.2	30.3 (7.2)	36.7 (8.8)
Crustacean Swimmer	Total	73.3	38.2 (8.8)	28.7 (9.9)	25	6.2 (6.2)	7.9 (7.9)	29.2	16.1 (6.4)	14.6 (6.4)
Fish undet.**	Total	13.3	8 (6.7)	6.7 (6.7)	75	43.8 (21.3)	28.9 (18)	50	20 (5.3)	13.3 (5.5)
Fish Crypto-B.	Total	-	-	-	-	-	-	33.3	14.7 (4.6)	24.2 (7.8)
Fish Necto-B	Total	13.3	3.9 (2.7)	8.2 (6.4)	50	37.5 (23.9)	54.8 (24.8)	4.2	4.2 (4.2)	4.2 (4.2)
MPO	*Corallina* sp.	6.7	1.1 (1.1)	0.1 (0.1)	-	-	-	4.2	1.2 (1.2)	0 (0)
MPO	*Cystoseira brachycarpa*	6.7	1.1 (1.1)	0.3 (0.3)	-	-	-	8.3	1.4 (1)	0.3 (0.3)
MPO	MPO undet.	6.7	1.7 (1.7)	0 (0)	-	-	-	4.2	0.6 (0.6)	0 (0)
MPO	*Posidonia oceanica*	6.7	1.1 (1.1)	0 (0)	-	-	-	-	-	-
Gastropoda	Gastropoda [1,2[	6.7	1.1 (1.1)	0 (0)	-	-	-	4.2	0.8 (0.8)	0.2 (0.2)
Gastropoda	Gastropoda [2,4[	6.7	3.3 (3.3)	1 (1)	-	-	-	-	-	-
Crustacean Walker	Majidae [2,4[	-	-	-	-	-	-	4.2	0.6 (0.6)	0.3 (0.3)
Crustacean Walker	Majidae [4,8[	13.3	2.4 (1.8)	4.6 (4.4)	-	-	-	8.3	2.2 (1.6)	0.8 (0.6)
Crustacean Walker	Majidae [8,+[	13.3	4.4 (3.4)	11.5 (7.9)	-	-	-	8.3	3.5 (2.5)	6.6 (4.6)
Crustacean Walker	Other Brachyura[4,8[	-	-	-	-	-	-	8.3	2 (1.5)	4.5 (3.4)
Crustacean Walker	Other Brachyura[8,+[	26.7	15.6 (7.7)	22.9 (10.3)	-	-	-	4.2	4.2 (4.2)	4.2 (4.2)

To be continued next page

Table S3: (continued)

		S. porcus (n = 15)			*S. cabrilla* (n = 4)			*S. scriba* (n = 24)		
(Very) broad Functional G.	Fine Functional G.	F	N mean (SE)	W mean (SE)	F	N mean (SE)	W mean (SE)	F	N mean (SE)	W mean (SE)
Crustacean Walker	Galatheoidea [2,4[	6.7	1.5 (1.5)	0 (0)	-	-	-	4.2	4.2 (4.2)	4.2 (4.2)
Crustacean Walker	Galatheoidea [4,8[	6.7	1.7 (1.7)	0 (0)	-	-	-	16.7	5.2 (2.6)	4.2 (3)
Crustacean Walker	Galatheoidea [8,+[	13.3	3 (2.1)	5.9 (5.1)	-	-	-	16.7	8.5 (4.7)	12.1 (5.9)
Crustacean Walker	Isopoda [2,4[	-	-	-	25	12.5 (12.5)	8.3 (8.3)	-	-	-
Crustacean Walker	Isopoda [4,8[	13.3	5.6 (3.9)	4.2 (3.1)	-	-	-	-	-	-
Crustacean Walker	Isopoda [8,+[	6.7	3.3 (3.3)	5.3 (5.3)	-	-	-	-	-	-
Crustacean Swimmer	Amphipoda [4,8[	13.3	2.4 (1.8)	1.9 (1.5)	-	-	-	-	-	-
Crustacean Swimmer	Caridea [1,2[	6.7	0.7 (0.7)	0 (0)	-	-	-	-	-	-
Crustacean Swimmer	Caridea [2,4[	26.7	4.9 (2.3)	0.6 (0.3)	-	-	-	4.2	1.4 (1.4)	0.2 (0.2)
Crustacean Swimmer	Caridea [4,8[	33.3	18.3 (8.1)	12.5 (7)	-	-	-	8.3	2.1 (1.5)	0 (0)
Crustacean Swimmer	Caridea [8,+[	33.3	11.9 (4.9)	13.7 (7)	25	6.2 (6.2)	7.9 (7.9)	20.8	12.6 (6)	14.4 (6.4)
Other invertebrates	Ectoprocta	6.7	1.7 (1.7)	0.2 (0.2)	-	-	-	-	-	-
Other invertebrates	Asterozoa [8,+[	-	-	-	-	-	-	4.2	4.2 (4.2)	4.2 (4.2)
Fish Crypto-B.	Blenniidae and Gobiidae [20,30]	-	-	-	-	-	-	8.3	3.5 (2.5)	2.8 (2.1)
Fish Crypto-B.	*Trypterigion* sp. [20,60]	-	-	-	-	-	-	29.2	11.2 (3.9)	21.4 (7.5)
Fish Necto-B	*Coris julis* [20,40]	-	-	-	50	37.5 (23.9)	54.8 (24.8)	-	-	-
Fish Necto-B	*Symphodus* spp. [20,30]	13.3	3.9 (2.7)	8.2 (6.4)	-	-	-	4.2	4.2 (4.2)	4.2 (4.2)

Figure S4: Draftsman's plots of posterior source contributions, showing interrelations between pairs of sources



Chapitre 6 (version française). Discussion générale et perspectives

Dans l'Infralittoral rocheux Méditerranéen, les grandes algues brunes du genre *Cystoseira* forment des habitats structurellement complexes, dénommés forêts à *Cystoseira*. Les forêts à *Cystoseira* sont considérées comme localement menacées dans l'ensemble du bassin Méditerranéen. A cause de nombreux facteurs de perturbations d'origine anthropique, les forêts à *Cystoseira* ont déjà disparu dans de nombreuses localités et sont en train de régresser dans d'autres. Elles ont été (sont) généralement remplacées par des habitats structurellement moins complexes tels que les *shrublands*, *turfs* et *barrens* (Cf. Chapitre 1). Le présent projet de thèse a visé à estimer les possibles conséquences pour les poissons de la régression des forêts à *Cystoseira* et à identifier les processus écologiques en cause. Pour cela, la structure des peuplements de poissons a été comparée entre les forêts à *Cystoseira* et des habitats structurellement moins complexes, puis certains processus écologiques pouvant contribuer à façonner les patrons de distribution spatiale des peuplements de poissons ont été étudiés. Une attention particulière fut portée à l'étude des processus liés à deux fonctions écosystémiques que les *Cystoseira* spp. peuvent potentiellement assurer : "formeur d'habitat" et "source de matière organique".

1 Les différences entre habitats et les processus sous-jacents

Nos inventaires de terrain (Chapitre 3) ont mis en évidence que les poissons sont plus diversifiés et abondants dans les forêts à *Cystoseira brachycarpa* comparés à des habitats adjacents de types *turf* et *barren*. Les poissons associés principalement aux forêts à *Cystoseira brachycarpa* incluent juvéniles et adultes de nombreuses espèces de poissons de petite taille, crypto-benthiques (*e.g.* Blenniidae, Gobiidae, Trypterigiidae) et necto-benthiques (principalement *Symphodus* spp.). Ces poissons se nourrissent principalement d'invertébrés de petite taille (*e.g.* copépodes, amphipodes) et sont donc communément appelés "mesocarnivores". Des juvéniles et adultes d'autres espèces plus grandes ont aussi été associés principalement aux forêts *à Cystoseira brachycarpa*, notamment *Serranus cabrilla*, *S. scriba* et *Scorpaena porcus*. Ces poissons se nourrissent de grands invertébrés (*e.g.* crabes, galatés) et de petits poissons (*e.g.* petits labres, Chapitre 5) et sont donc communément appelés "macrocarnivores". Ainsi, des poissons meso- et macro-carnivores, qui sont respectivement proies et prédateurs, cohabitent dans les forêts à *Cystoseira brachycarpa*.

Pour mieux comprendre les raisons de ces plus grandes densités de meso- et macro-carnivores dans les forêts à *Cystoseira brachycarpa,* nous avons cherché si cela était lié, au moins en partie, à la possible fonction "formeur d'habitat" de *Cystoseira brachycarpa*. Pour cela, nous avons regardé si la complexité structurelle de l'habitat avait des effets sur les interactions proies-prédateurs et sur les décisions prises par les poissons lorsqu'ils choisissaient leur espace de vie.

1.1 Différences de mortalité

Des taux de mortalité (induite par prédation et/ou par famine) inférieurs dans les forêts à *Cystoseira brachycarpa* peuvent contribuer à façonner les différences de densités entre habitats. En se focalisant sur les interactions proie-prédateur entre poissons méso- et macro-carnivores, nous nous sommes intrinsèquement focalisés sur la mortalité des méso-carnivores induite par prédation et, dans une certaine mesure, sur la mortalité des macro-carnivores induite par famine.

Dans nos expériences de survie réalisées en aquariums (Chapitre 4), une proie *Symphodus ocellatus* face à un prédateur *Serranus cabrilla* ou face à un prédateur *Scorpaena porcus*, survivait plus longtemps dans l'habitat artificiel de type forêt à *Cystoseira* que dans les habitats artificiels de types *shrubland* et *barren*. Ces analyses de survie, complétées par des observations comportementales, ont démontré que (1) la complexité structurelle des *Cystoseira* spp. augmente la capacité de *S. ocellatus* à éviter / se cacher / s'échapper face à un prédateur (*i.e.* l'efficacité de son comportement anti-prédateur), ou de l'autre point de vue (2) la complexité structurelle des *Cystoseira* spp. réduit la capacité des prédateurs à détecter / localiser / poursuivre / capturer un *S. ocellatus* (*i.e.* l'efficacité de son comportement de chasse).

Cependant, cette découverte n'implique pas nécessairement qu'en milieu naturel, *S. ocellatus* (et les autres poissons proies) survivent plus longtemps dans les forêts à *Cystoseira*, ni que *S. cabrilla* et *S. porcus* (et les autres poissons prédateurs) ne réussissent pas à subvenir à leurs besoins alimentaires dans les forêts à *Cystoseira*. Nos expériences en aquariums n'ont pas considéré les densités naturelles des poissons prédateurs ni des poissons proies et des autres proies visées par les poissons prédateurs (*e.g.* crustacés). Ainsi, les résultats de nos expériences de survie ne peuvent pas refléter la véritable intensité des interactions létales entre poissons proies et prédateurs. Ceci peut être illustré par l'analyse intégrative des nos résultats obtenus lors nos inventaires de terrain (Chapitre 3), de nos expériences en aquariums (Chapitre 4) et de notre analyse du réseau trophique (Chapitre 5), qui souleva trois points:

- Les densités de macrocarnivores sont plus élevées dans les forêts à *Cystoseira* (Chapitre 3). Cela augmente le risque pour les poissons proies de rencontrer des prédateurs et par conséquent, ceci peut contrebalancer l'effet positif qu'a *Cystoseira* spp., en tant que formeur d'habitat, sur l'efficacité du comportement anti-prédateur des poissons proies (Chapitre 4).
- L'analyse des habitudes alimentaires des macrocarnivores habitant les forêts *à Cystoseira brachycarpa* (Chapitre 5) a révélé que les macrocarnivores réussissent à se nourrir de petits poissons necto-benthiques, particulièrement le macrocarnivore *S. cabrilla* dont les petits labridés représentaient 80% de son régime alimentaire. La prédation est donc effective, même si l'efficacité de prédation est diminuée par la complexité structurelle de *Cystoseira* spp.. Cela peut être dû aux plus grandes densités de petits labridés dans les forêts *à Cystoseira brachycarpa* (Chapitre 3) qui peuvent augmenter le nombre de proies rencontrées par le prédateur (fort taux de rencontre), ce qui peut compenser l'effet négatif de *Cystoseira* spp. sur la capacité du prédateur à capturer la proie rencontrée (faible taux de succès d'attaque).
- Les macrocarnivores se nourrissent également d'autres proies que les petits poissons dans les forêts *à Cystoseira brachycarpa* (Chapitre 5). Par exemple, les crustacés

représentent plus de 80% du régime alimentaire de *S. porcus* et environ 20% de celui de *S. cabrilla*. En considérant que les densités de crustacés sont probablement plus importantes dans les forêts à *Cystoseira brachycarpa* que dans les habitats structurellement moins complexes (voir références dans les chapitres précédents), cela peut fournir aux macrocarnivores un large choix de proies potentielles et ainsi contribuer à réduire la pression de prédation subie par les poissons proies dans les forêts à *Cystoseira brachycarpa.*

Nota bene : nous n'avons pas pu comparer le régime alimentaire des macrocarnivores entre habitats. En effet, dans notre localité d'étude (Calvi, Corse), les habitats rocheux autres que la forêt à *Cystoseira* (*shrubland*, *turf*, *barren*) ne couvrent que des petites surfaces (*i.e.* patchs ≈ 30 x 30 m²), probablement bien inférieures aux domaines vitaux de ces poissons. Les poissons rencontrés dans ces patchs étaient peu nombreux et probablement n'y résidaient pas à temps plein. La configuration du paysage était donc inappropriée pour l'étude des régimes alimentaires spécifiques à chaque habitat.

Ainsi, la présente étude augmente notre connaissance des effets de la complexité structurelle de l'habitat sur les interactions létales et comportementales entre poissons proies et prédateurs. Toutefois, elle ne permet pas d'estimer si dans l'ensemble, il existe des différences de mortalité entre habitats. Comparer la véritable intensité de l'interaction létale entre méso- et macro- carnivores ne peut être accompli que par l'emploi d'expériences *in situ* qui doivent inclure les densités spécifiques à chaque habitat, des poissons prédateurs, des poissons proies, et des autres proies visées par les poissons prédateurs. De plus, pour estimer plus généralement la contribution d'éventuelles différences de mortalités entre habitats dans le façonnement des patrons de distributions des poissons, la mortalité des mésocarnivores induite par famine et la mortalité des macrocarnivores induite par prédation (par des prédateurs encore plus grands) doivent être également considérées.

1.2 Sélection de l'habitat

La sélection de l'habitat est une décision prise par chaque individu quant à l'environnement dans lequel il décide d'habiter. La prise de décision est stimulée par des paramètres environnementaux indiquant à l'individu les coûts et bénéfices pour son fitness qui sont associés au fait d'habiter dans un habitat donné. Les paramètres environnementaux utilisés par les individus lorsqu'ils sélectionnent leur habitat peuvent inclure notamment la complexité structurelle de l'habitat, la disponibilité en nourriture et le risque de prédation.

Nos expériences de choix d'habitat réalisées en aquariums (Chapitre 4), ont démontré que des individus isolés de *S. ocellatus*, *S. cabrilla* et *S. porcus*, lorsqu'ils ont le choix entre la forêt à *Cystoseira* artificielle ou le *shrubland* artificiel, préfèrent la forêt à *Cystoseira*, c'est-à-dire l'habitat le plus complexe structurellement (bien que nous ne puissions pas exclure un possible artefact pour *S. porcus*). Lorsqu'une proie et un prédateur sont ensemble dans " l'arène à choix ", tous deux continuent à préférer la forêt à *Cystoseira* (voir toutefois la discussion du Chapitre 4 pour le couple *S. ocellatus* - *S. porcus*). Cela démontre que (1) la complexité structurelle de l'habitat est un paramètre qui à lui seul déclenche un choix chez les poissons, qui ont ici une préférence pour les habitats structurellement complexes, (2) le risque de prédation ne semble pas influencer la préférence d'habitat de *S. ocellatus*, (3) la présence de proie n'est pas indispensable au choix d'habitat fait par le prédateur.

La complexité structurelle de la forêt à *Cystoseira* est suffisante pour attirer les poissons, *i.e.* le choix de l'habitat n'est pas une réaction à la présence de proies et/ou de prédateurs. La complexité structurelle de l'habitat serait un indice utilisé par le poisson informant sur la présence de proie et prédateurs potentiels. La sélection d'habitat serait donc plutôt un comportement proactif appris et/ou sélectionné au cours de l'évolution *via* des pressions sélectives liées à la prédation ou à la prise alimentaire, *i.e.* des réminiscences d'interactions proie-prédateur passées.

Nous n'avons pas estimé les possibles effets de la disponibilité en nourriture (invertébrés) sur le choix d'habitat fait par *S. ocellatus*, ni les possibles effets d'un risque de prédation (par des prédateurs encore plus grands) sur les choix d'habitats de *S. cabrilla* et *S. porcus*. Cependant, ces éventuels effets ne devraient vraisemblablement pas inverser les préférences d'habitats observées durant cette étude. En considérant que les invertébrés sont probablement plus abondants dans les forêts à *Cystoseira* (références dans les chapitres précédents), cette plus grande disponibilité en nourriture dans la forêt ne devrait pas inhiber la préférence de *S. ocellatus* pour la forêt déjà constatée en absence de nourriture. De même, il apparait vraisemblable que des macrocarnivores menacés par des prédateurs encore plus grands resteraient dans la forêt de façon à utiliser, à leur tour, la complexité structurelle comme abri anti-prédation.

Ainsi, la présente étude suggère que les plus grandes densités à la fois de proies et de prédateurs dans les forêts à *Cystoseira* peuvent résulter, au moins en partie, d'immigrations nettes des individus qui sont attirés par la plus grande complexité structurelle fournie par *Cystoseira* spp. Il serait nécessaire de réaliser d'autres expériences (1) *in situ* où tous les facteurs influençant potentiellement la sélection d'habitat pourraient interagir, et (2) *ex situ* en offrant le choix aux poissons entre toutes les combinaisons possibles de types d'habitats, de présence/absence de nourriture et de prédateurs, de façon à mieux comprendre les mécanismes écologiques et évolutifs qui sont impliqués dans l'apparition et la persistance des comportements quant à la sélection de l'habitat.

1.3 *Cystoseira* spp. en tant que source de matière organique

Nous avons étudié l'importance potentielle de *Cystoseira brachycarpa* en tant que source de matière organique en utilisant des analyses de compositions isotopiques du carbone et de l'azote (Chapitre 5). Nous avons trouvé que la matière organique particulaire (POM) et/ou *Cystoseira brachycarpa* et/ou certaines autres macroalgues pouvaient potentiellement être d'importantes sources soutenant le réseau trophique (incluant les peuplements de poissons). Ces potentielles sources de matière organique passeraient par les parcours trophiques pélagiques et/ou benthiques (*via* les consommateurs primaires) et/ou passeraient par la boucle microbienne en tant que source de détritus. A cause de compositions isotopiques similaires entre ces potentielles sources, nous n'avons pas pu identifier les différents parcours trophiques ni le rôle de *C. brachycarpa* en tant que source soutenant les peuplements de poissons. Face aux ambiguïtés liées à des compositions isotopiques du carbone et de l'azote similaires entre sources, l'addition du souffre dans les analyses isotopiques et l'utilisation de l'approche complémentaire qu'est l'analyse des acides gras, pourraient aider à identifier les sources de matière organique à la base du réseau trophique de l'écosystème forêt à *Cystoseira brachycarpa*.

2 Des patrons de distributions et processus observés aux conséquences de la dégradation des forêts à *Cystoseira*.

Dans la présente étude, nous avons décrit des distributions (dans l'espace) de poissons et leurs processus sous-jacents, dans le but ultime de déduire quelles étaient les conséquences (au cours du temps) pour les poissons de la dégradation des forêts à *Cystoseira*. A cause du manque de données historiques concernant la structure des peuplements de poissons avant que les forêts à *Cystoseira* ne disparaissent de certaines localités, nous n'avons pas pu utiliser l'approche la plus directe et la plus puissante: *Before-After-Control-Impact*. Nous avons donc utilisé une approche *Space-for-Time* (voir Chapitre 1). Le principe de l'approche *Space-for-Time* est que les différences spatiales observées entre habitats peuvent refléter des différences temporelles entre avant et après que les habitats aient changé.

La distribution spatiale des poissons entre habitats et les processus sous-jacents sont vraisemblablement dépendants de la configuration du paysage sous-marin. Dans un paysage composé de patchs de différents habitats qui sont petits et alternés dans l'espace (*interspersed*), il est raisonnable de considérer que les mouvements des poissons entre patchs sont possibles. Par conséquent, la sélection de l'habitat peut avoir une importance considérable dans le façonnement des patrons de distribution des poissons entre ces patchs de différents habitats. Au contraire, dans un paysage où chaque habitat est représenté par une seule grande surface, les habitats sont ségrégés et les poissons peuvent avoir des difficultés à trouver l'habitat qu'ils préfèrent. Par conséquent, la sélection d'habitat pourrait avoir un rôle moindre dans le façonnement des patrons de distribution entre habitats et les différences de mortalité entre habitats pourraient avoir une plus grande importance. En supposant cela, une approche *Space-for-Time* consistant en la comparaison de différents habitats qui s'étendent chacun sur de vastes surfaces, devrait refléter plus fidèlement les véritables conséquences (temporelles) des changements d'habitats. En effet, les grandes surfaces privilégient les processus propres à chaque habitat (qui peuvent être similaires aux processus impliqués dans les changements d'habitats) et ne privilégient pas les processus spatiaux tels que la sélection d'habitat.

Comme discuté dans le Chapitre 3, la distribution actuelle des habitats dans le bassin Méditerranéen implique que la comparaison d'habitats qui s'étendent sur de vastes surfaces ne peut être faite que par la comparaison de sites très distants. Cela revient par exemple à comparer les forêts à *Cystoseira* de Corse et de Minorque aux *shrublands* de deux localités situées sur les côtes continentales. Cependant, une telle étude à large échelle spatiale est sensible aux confusions d'effets, dus à d'autres facteurs que l'habitat, qui peuvent induire également des variations spatiales. Avec un tel dessin d'échantillonnage, il deviendrait donc difficile de répondre à la question : *la structure des peuplements de poissons est-elle différente entre forêts et* shrublands*, ou plutôt est-elle différente entre îles et continent ?* Ainsi, avec une approche *Space-for-Time,* il est primordial d'échantillonner un très grand nombre de localités, chacune présentant un paysage dominé par un seul habitat, et autant que possible d'alterner spatialement les localités présentant des habitats différents. Dans le présent projet de thèse, les contraintes logistiques n'ont pas permis de réaliser un tel dessin d'échantillonnage. C'est pourquoi nous avons utilisé un dessin d'échantillonnage où le facteur habitat est niché au sein du facteur localité (voir Chapitre 3), afin de limiter les possibles confusions d'effets. Pour ce faire, nous avons tenté de sélectionner des localités où les habitats forêts à *Cystoseira*, *shrubland*, *turf* et *barren* étaient tous présents et où chaque habitat couvraient des surfaces les plus grandes possibles. Cela nous a conduit à comparer les habitats au sein de localités situées en Corse et à Minorque, où le paysage est dominé par les forêts à *Cystoseira* et où les autres habitats (principalement des *barrens*) ne couvrent que des petites à moyennes surfaces (environ 30 x 30 m²) imbriquées au milieu de vastes étendues de forêts à *Cystoseira*. Avec une telle configuration paysagère, la sélection d'habitat par les poissons a probablement un rôle important dans les patrons de distribution que nous avons observés.

Notre inventaire de terrain a montré que les poissons sont plus diversifiés et abondants dans les forêts à *Cystoseira brachycarpa* comparés aux habitats adjacents de type *turf* et *barren*. Nos expériences en aquariums suggèrent que la sélection d'habitat et les différences de mortalité entre habitats, peuvent toutes deux contribuer à façonner les différences d'abondances observées entre habitats. Toutefois, la contribution relative de la sélection d'habitat *vs* différence de mortalité (dans le façonnement des patrons de distribution) reste inconnue. Par conséquent, le présent travail ne permet pas d'estimer les conséquences pour les poissons de la régression des forêts à *Cystoseira*.

Pour expliquer cette dernière affirmation, considérons une hypothétique localité où la situation actuelle serait la suivante : une forêt à *Cystoseira* et un *barren* sont présents et chaque habitat couvre la moitié de la localité ; et considérons une hypothétique espèce de poisson qui serait la plus abondante dans la forêt à *Cystoseira.* Ensuite, posons deux scénarios quant à la contribution relative de la sélection d'habitat *vs* différence de mortalité dans le façonnement des patrons de distribution, et envisageons pour chaque scénario les conséquences pour les poissons si dans le futur la forêt à *Cystoseira* disparaissait totalement de la localité en étant remplacée par du *barren* (Figure 1).

- Scénario 1: les poissons ne sélectionnent pas un habitat en particulier (pas de préférence d'habitat), le patron de distribution actuel n'est donc dû qu'à une plus grande mortalité dans le *barren*. Si la forêt à *Cystoseira* devient un *barren*, les poissons vont subir une plus grande mortalité dans l'ensemble de la localité (qui n'est qu'un grand *barren*) et les conséquences pour la densité de poissons peuvent être dramatiques.
- Scénario 2: la mortalité des poissons est équivalente dans les deux habitats et le patron de distribution actuel n'est donc dû qu'à une immigration des poissons dans la forêt à *Cystoseira* due à leur préférence d'habitat. Si la forêt à *Cystoseira* se dégrade en *barren*, les poissons n'auront plus le choix d'habitat et ils vont se redistribuer dans l'ensemble de la localité qui n'est qu'un grand *barren*. Puisque la mortalité est équivalente entre forêt à *Cystoseira* et *barren*, les conséquences pour les abondances de poissons devraient être négligeables à l'échelle de temps écologique. Toutefois, les poissons vivront dans le *barren* au lieu de la forêt à *Cystoseira*, leur utilisation des micro-habitats et leurs interactions comportementales seront différentes. Cela pourrait affecter les pressions sélectives et donc les processus liés à la génération et au maintien de la biodiversité.

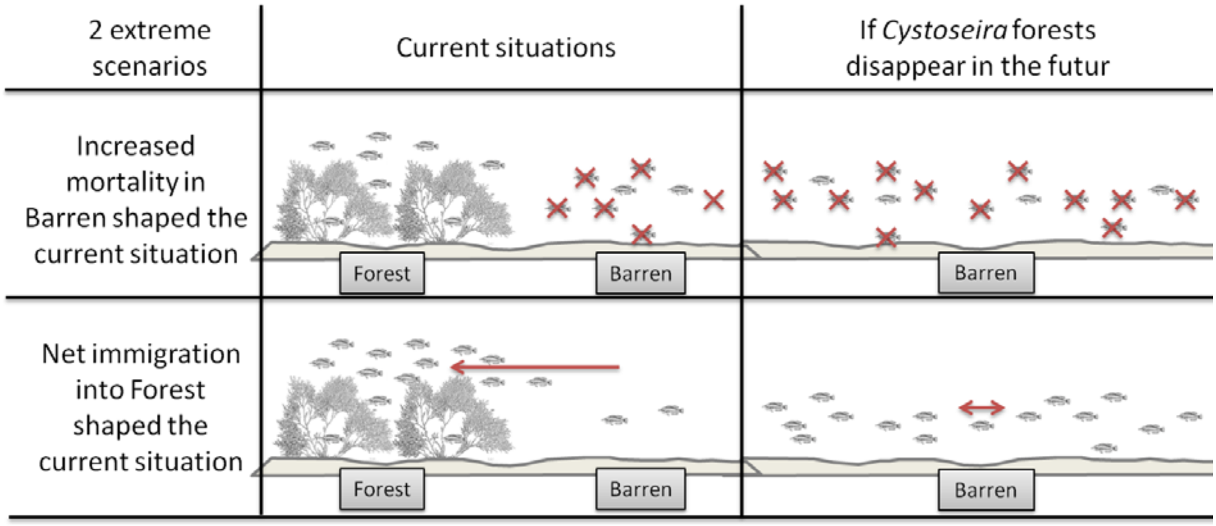


Figure 1: Deux scénarios extrêmes quant à la contribution relative de la sélection d'habitat *vs* différence de mortalité dans le façonnement des patrons de distributions observés actuellement. Pour chaque scénario, les **conséquences pour les poissons** sont envisagées si dans le futur la forêt à *Cystoseira* se dégrade en *barren*.

Il est important de souligner que ces deux scénarios ne considèrent pas tous les facteurs qui peuvent influencer les possibles changements de mortalité et de sélection d'habitats induits par le changement d'habitat. Par exemple, les proies et les prédateurs devraient eux aussi répondre au changement d'habitat. Les deux scénarios et leurs conséquences énoncés ci-dessus sont donc très imprécis. Ils ont été énoncés d'une façon simpliste dans le but d'illustrer à quel point il est important de connaitre la contribution relative de la sélection d'habitat *vs* différence de mortalité, lorsque nous cherchons à prédire les conséquences de la régression des forêts à *Cystoseira* en se basant sur l'interprétation de patrons de distributions observés actuellement (*i.e.* au travers d'une approche *Space-for-Time*).

3 Conclusion

Bien que le présent travail ne permette pas véritablement d'estimer les conséquences pour les poissons de la régression des forêts à *Cystoseira*, il met en évidence que les poissons survivent mieux et/ou préfèrent habiter dans les forêts à *Cystoseira*. Cela serait dû, au moins en partie, à la fonction de "formeur d'habitat" des *Cystoseira* spp. qui fournissent une grande complexité structurelle à cet habitat et ainsi régissent les interactions létales et/ou comportementales entre poissons. Ceci souligne la nécessité de développer de meilleures mesures de gestion et de conservation des forêts à *Cystoseira* encore existantes ainsi que des méthodes (*e.g.* ingénierie écologique) pour la restauration des forêts à *Cystoseira* déjà disparues (Gianni *et al.* 2013).

4 Perspectives

Pour mieux comprendre les fonctions écologiques de *Cystoseira* spp. et prévoir les conséquences d’éventuels futurs déclins des forêts à *Cystoseira*, des études complémentaires devraient notamment : (1) étendre les inventaires de biodiversité à de plus larges échelles spatiales et temporelles, (2) étudier de manière plus approfondie les interactions létales et comportementales entre proies et prédateurs et entre compétiteurs, et (3) identifier les sources de matière organique qui soutiennent le réseau trophique spécifique à chaque habitat.

Pour ce dernier point, nous avons déjà proposé la combinaison d'analyses isotopiques du carbone de l'azote et du soufre et d'analyses des acides gras. Pour les deux premiers points, voici quelques remarques sur les possibles approches à employer.

4.1 Inventaires et suivis de la biodiversité

Afin d'obtenir une image plus globale de la structure et du fonctionnement des écosystèmes rocheux, il serait nécessaire de :

- Réaliser des inventaires dans de nombreuses localités, diurnes et nocturnes à plusieurs occasions durant chaque saison, de façon à prendre en compte les variabilités spatiales et temporelles (*e.g.* nycthémérales, saisonnières).
- Réaliser des inventaires exclusivement dans des habitats couvrant de grandes surfaces de façon à éviter les effets de bords (*Edge effects,* Chapitre 2).
- Réaliser des inventaires de tous les compartiments trophiques (incluant les invertébrés, proies de nombreuses espèces de poissons) de façon à mieux estimer la structure trophique des écosystèmes.
- Utiliser de multiples méthodes d'échantillonnages, chacune adaptée à un compartiment, telles que l'*Enclosed Anesthetic Station* pour échantillonner les poissons crypto-benthiques (*Cf.* Chapitre 3).

De plus, des programmes de suivis à long terme doivent être mis en place. L'actuel manque de série temporelle ne permet pas d’estimer clairement les conséquences des déclins passés des forêts à *Cystoseira*. Mettre en place de tels suivis dès maintenant permettrait au moins de détecter au plus tôt les possibles futurs changements d'habitats et leurs conséquences pour les communautés fauniques associées.

4.2 Etudier les processus écologiques

Pour prévoir les conséquences de possibles futurs régressions des forêts à *Cystoseira*, il serait avantageux d'estimer la contribution relative de la sélection d'habitat *vs* différence de mortalité dans le façonnement des patrons de distributions observés actuellement : objectif 1.

Pour mieux comprendre ces processus, il serait avantageux d'identifier les facteurs qui les affectent, dont la complexité structurelle de l'habitat, la disponibilité en nourriture et le risque de prédation : objectif 2.

Pour remplir l'objectif 1, il serait nécessaire de réaliser des expériences qui incluent les densités de proies, de prédateurs et de compétiteurs spécifiques à chaque habitat. Il est quasiment impossible de recréer en aquarium ces conditions naturelles. Des expériences *in situ* sont donc l'unique solution. Les approches de type Capture-Marquage-Recapture et *Sonar tracking* peuvent être appropriées. La méthode Capture-Marquage-Recapture est couramment utilisée pour estimer la croissance, la mortalité et les mouvements des organismes (et leur sélection d'habitat) (Chapman & Kramer 2000). Le *Sonar tracking* est également très efficace pour suivre au cours du temps les mouvements des organismes (Koeck *et al.* 2013). Toutefois, ces approches sont corrélatives et ne permettent pas de contrôler les différents facteurs supposés affecter la croissance, la mortalité et la sélection d'habitat des organismes. Elles sont donc inappropriées pour remplir l'objectif 2.

Pour remplir l'objectif 2, les expériences doivent consister en un dessin expérimental orthogonal dont les traitements sont les combinaisons de chaque facteur : type d'habitat, présence/absence de proie, de prédateurs, de compétiteurs (Horinouchi *et al.* 2013). C'est un réel défi pour les expérimentateurs. Une approche couramment employée pour comparer entre traitements les taux de mortalités (et éventuellement de croissance) est le *tethering* qui consiste à maintenir les organismes à un endroit donné (*e.g.* dans un habitat particulier) en les attachant à l'aide d'une ficelle (Peterson & Black 1994). Toutefois, nos expériences en aquariums (Chapitre 4) ont montré que le comportement anti-prédateur de *S. ocellatus* consiste notamment en des mouvements verticaux et horizontaux dans et au travers les différentes strates des habitats (*e.g.* pour la forêt : pleine eau, canopée et sous-bois). Il est vraisemblable qu'un *S. ocellatus* attaché au bout d'une ficelle sera plus empêtré dans la forêt à *Cystoseira* que dans un *barren* ou un *shrubland*, lorsqu'il devra mettre en œuvre une tactique d'anti-prédation. Dans la forêt à *Cystoseira*, la ficelle risque de s'emmêler autour des troncs et branches rigides de *Cystoseira* spp., bien plus qu'elle ne s'emmêlerait autour des thalles souples formant les habitats de type *shrubland*. Cette interaction prévisible entre l'intervention (attacher le poisson) et le traitement "type d'habitat" (*i.e.* un artefact) décourage l'utilisation de *tethering* pour le système étudié (Peterson & Black 1994). Des expériences utilisant des cages pour exclure les prédateurs ont également été utilisées pour estimer l'effet de prédation. Toutefois, les cages d'exclusion empêchent souvent les prédateurs d'entrer mais permettent aux proies d'entrer et sortir, ce qui peut générer d'important artefacts : *e.g.* les proies rentrent massivement car attirées par la structure de la cage (Hindell *et al.* 2000). Ainsi, il vaut mieux utiliser des cages d'inclusion qui empêchent toute migration de proie et prédateur (*i.e.* un mésocosme). Les mésocosmes peuvent également être transformés en arène à choix pour estimer les différents facteurs influençant la sélection d'habitat (Figure 2).

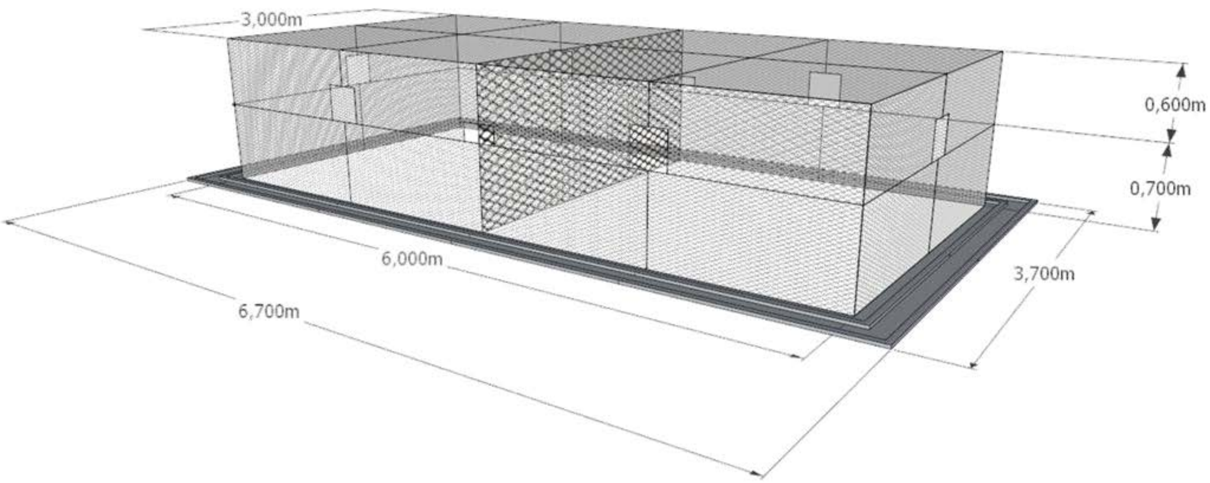


Figure 2. Schéma d'une arène à choix *in situ*. L'ensemble de la cage ne permet à aucun poisson de rentrer ou sortir. La cage est constituée de deux compartiments séparés par une grillage assez fin pour empêcher les prédateurs de changer de compartiment, mais assez gros pour permettre aux poissons proies de passer au travers et donc de choisir leur compartiment. Ce dispositif permet de contrôler la densité de prédateurs dans chaque compartiment de façon à tester l'effet que les prédateurs ont sur la sélection d'habitat des proies.

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Chapter 6 (english version). General discussion and perspectives

In Mediterranean subtidal rocky reefs, large brown macroalgae of the genus *Cystoseira* form structurally complex habitats, called *Cystoseira* forests. *Cystoseira* forests are considered as locally threatened in the whole Mediterranean Basin due to various anthropogenic stressors. *Cystoseira* forests already collapsed in numerous localities and are regressing in others. They can be replaced by less structurally complex habitat-types such as shrublands, turfs and barren grounds. The present PhD work aimed to compare fish assemblage structure between *Cystoseira* forests and less structurally complex habitats, and to investigate the ecological processes that may contribute to shape the spatial differences in fish assemblage structure. Special attention was paid to the processes related to two putative functions of *Cystoseira* spp.: 'habitat-former' and 'source of organic material'.

1 The spatial differences among habitat-types and underlying processes

Our field surveys (Chapter 3) evidenced that fish are more diversified and abundant in *Cystoseira brachycarpa* forests compared to adjacent barrens and turfs. Species associated primarily to *Cystoseira brachycarpa* forests include juveniles and adults of numerous small-sized species, crypto-benthic (*e.g.* Blenniidae, Gobiidae, Trypterigiidae) and necto-benthic (mainly *Symphodus* spp.). These species feed mainly on small-sized invertebrates and are therefore referred as mesocarnivores. Juveniles and adults of larger-sized species were also primarily associated to *Cystoseira brachycarpa* forests, including *Serranus cabrilla*, *S. scriba*, and *Scorpaeana porcus*. These species prey upon large-sized invertebrates and on small-sized fish (Chapter 5), and are therefore referred as macrocarnivores. Therefore, meso-and macro-carnivorous fish, respectively prey and predatory fish, cohabit in *Cystoseira brachycarpa* forests.

We tested if the higher densities of both mesocarnivores and macrocarnivores fish in *Cystoseira brachycarpa* forests were related, at least in part, to the effects of habitat structural complexity upon their decision making as concerns habitat selection and upon their prey-predator interactions. For doing so, we set-up tank-based habitat choice and survival experiments (Chapter 4), and we estimated macrocarnivores' feeding habits in *C. brachycarpa* forest by using stomach contents and stable isotope mixing models (Chapter 5).

1.1 Differential mortality

Reduced predation- and starvation- induced mortality in *Cystoseira* forests may contribute to shape fish density patterns between habitats. By focusing on prey-predator interactions between meso- and macro- carnivorous fish, we inherently focused on predation-induced mortality of mesocarnivores and in some extent on starvation-induced mortality of macrocarnivores.

In our tank-based survival experiments (Chapter 4), one prey *Symphodus ocellatus* survived longer in artificial *Cystoseira* Forest than in artificial Shrub or Barren, face to one predator *Serranus cabrilla* as well face to one predator *Scorpaena porcus*. These survival analyses complemented with behavioral observations, demonstrated that (1) *Cystoseira* spp. structural complexity increases *S. ocellatus* ability to hide/escape/avoid face to one predator (*i.e.* the efficiency of its anti-predator behaviors), or from the other perspective (2) *Cystoseira* spp. structural complexity reduces predators ability to detect/locate/pursue/capture one *S. ocellatus* (*i.e.* the efficiency of their foraging behaviors).

However, this does not necessarily imply that in the field *S. ocellatus* (and other prey fish) better survive in *Cystoseira* forests nor that *S. cabrilla* and *S. porcus* (and other predatory fish) don't effectively feed in *Cystoseira* forests. Our tank experiments did not consider natural habitat-specific densities of predatory fish, prey fish, and the other prey targeted by macrocarnivores (*e.g.* crustacean). Therefore, our results cannot reflect the real strength of lethal prey-predator interactions in the field. This may be exemplified by the integration of our results obtained by tank experiments, field surveys and food web analysis, which raised 3 points:

- Macrocarnivores densities are higher in *Cystoseira* forests (Chapter 3). This increases risk for prey fish of encountering predators and consequently, this may counterbalance the positive effect of *Cystoseira* spp. on prey fish anti-predator behaviors' efficiency.
- Feeding habit analyses of macrocarnivores inhabiting *Cystoseira brachycarpa* forests (Chapter 5) revealed that macrocarnivores succeed to prey upon small necto-benthic fish, especially *S. cabrilla* for whom small labrids was more than 80% of its diet. Predation is therefore effective, even if predation efficiency is lowered by *Cystoseira* spp. structural complexity. This may be due to the higher densities of small labrids in *Cystoseira* forest that increase encounter rates and overcome the reduced capture-success rates.
- Macrocarnivores feed also upon other prey in *Cystoseira brachycarpa* forests (Chapter 5). For instance, crustacean was more than 80% of *S. porcus* diet and was around 20% of *S. cabrilla* diet. Considering that crustacean densities are possibly higher in *Cystoseira* forests than in less structurally habitats, this may provide macrocarnivores with a large choice in prey items and contribute to decrease the predation pressure that undergoes prey fish in *Cystoseira* forests.

NB: We could not compare macrocarnivores feeding habits between habitats. Indeed, in our study locality in NW Corsica, rocky habitats other than *Cystoseira* forest (e.g. Barren and Turf) covered too small areas relatively to the home range of these fish species. Fish were scarce and unlikely to inhabit strictly in these patches. The seascape configuration was therefore inappropriate for assessing their feeding habit from an habitat perspective.

Hence, the present work gives some new insights on the effects of habitat structural complexity on the different sequential stages of prey-predator interactions between meso- and macro- carnivores. But it did not allow to assess whether as a whole differential predation-induced mortality of prey fish and differential starvation-induced mortality of predatory fish contribute to shape differences in density patterns between habitats. Comparing reliably the strength of meso-macro carnivores lethal interactions between habitats may be accomplished only through field-based predation experiments that must include the habitat-specific densities of prey fish, predatory fish, and other prey targeted by predators. Moreover, for estimating more generally the putative contribution of differential mortality in shaping fish distribution patterns, starvation-induced mortality of mesocarnivores and predation-induced mortality of macrocarnivores should also be investigated.

1.2 Habitat selection

Habitat selection equates with active and adaptive choice of habitat (net immigration) based on proximate cues that reliably inform individuals of the fitness costs and benefits associated with inhabiting a given habitat. Proximate cues used by animals for selecting habitats may include notably habitat structural complexity, food availability and predation risk.

In our tank-based habitat choice experiments (Chapter 4), we found that isolated individuals of *S. ocellatus*, *S. cabrilla* and *S. porcus* preferred the structurally complex (artificial) *Cystoseira* Forest over the less complex artificial Shrub (even though for *S. porcus* we cannot exclude a possible artifact effect). When prey and predator were together in the choice arena, they still preferred the Forest (however see discussion about *S. ocellatus* - *S. porcus* in Chapter 4). This evidenced that (1) habitat structural complexity solely is enough for attracting both prey and predatory fish, (2) predation risk does not seem to affect prey habitat selection, and (3) food availability does not seem to affect predator habitat selection.

We did neither assess the putative effects of food availability (invertebrates) on *S. ocellatus* habitat selection, nor the putative effects of predation risk (from higher-level predators) on *S. cabrilla* and *S. porcus* habitat selections. But these possible effects are unlikely to reverse their observed habitat preferences. Considering that invertebrates are more abundant in *Cystoseira* forest (references in previous Chapters), this higher food availability is unlikely to inhibit *S. ocellatus* preference for forest. As well, it might be considered that macrocarnivores threatened by higher-level predators would remain in *Cystoseira* forest for taking advantage of the high structural complexity as shelter.

From these perspectives, the decision-making of *S. ocellatus*, *S. cabrilla* and *S. porcus* to move inside artificial *Cystoseira* forest during our tank experiments, even if their respective prey and predators were absent (isolated individuals), might be a proactive behavior learned and/or selected through predation and/or foraging pressures, *i.e.* a ghost of past prey-predator interactions.

The present work suggests that the higher densities of both prey and predatory fish in *Cystoseira* forests may result from, at least in part, a net immigration of individuals due to their preference for the habitat structural-complexity provided by *Cystoseira* spp. Further experiments including all combinations of food availability, predation risk and habitat structure would be required for (1) verifying our results in the field, where all factors putatively affecting habitat selection may interact, and (2) better understanding the ecological-behavioral and evolutionary mechanisms involved in the appearance and maintenance of fish behaviors as regards habitat selection.

1.3 *Cystoseira* spp. as primary producer

We investigated the possible importance of *Cystoseira brachycarpa* as source of organic material for the food web using stable isotope analyses (Chapter 5). We found that POM and/or *Cystoseira brachycarpa* and/or some other benthic primary producers were possibly important sources sustaining the fish assemblages, directly as prey of pelagic and benthic primary consumers, and/or indirectly as sources of detritus. Nevertheless, due to similarities in isotopic compositions of these putative sources, we could neither assess the different trophic pathways nor the possible trophic role of *C. brachycarpa* in sustaining fish assemblage. Against the ambiguity associated with similar carbon and nitrogen stable isotopes compositions among sources, the addition of sulfur in stable isotopes analyses and the complementary analysis of fatty acid biomarkers could help identifying the sources of organic matter that sustain fish assemblages in *C. brachycarpa* forest.

2 From the observed spatial patterns and processes to the impacts of habitat-shifts

The present work compared spatial distribution patterns and their underlying processes, intending ultimately to shed some lights on the putative past and present impacts of *Cystoseira* forest losses on fish assemblages. Due to the lack of historical data about fish assemblage structures before *Cystoseira* forests disappeared from some areas, we could not use a 'Before-After-Control-Impact' approach, which is the most straightforward and powerful approach for assessing an impact. We therefore used a 'space for time' approach. The rational of this approach is that the observed spatial differences between habitat-types and their underlying processes, possibly reflect temporal differences between before and after *Cystoseira* forest collapsed and their underlying processes.

Spatial distribution of fish among habitat-types and the underlying processes are likely dependent upon the seascape configuration. In a seascape composed by small interspersed patches of the different habitat-types, it is reasonable to consider that movements of fish across patches are possible. Consequently, habitat selection may possibly have an important contribution in structuring fish distribution patterns among patches of different habitat-types, as well possible edge effects (see Chapter 2). On the contrary, in a seascape where each habitat-type is represented by a single large area, habitat-types are segregated and this may reduce fish ability to find out its favored habitat. Consequently, differential mortality among habitat-types may possibly have a more important contribution in structuring fish distribution patterns. From this perspective, a 'space-for-time' approach comparing habitats that extend over larger areas should reflect more closely what are the effective (temporal) impacts of *Cystoseira* forests losses, since larger areas are primarily affected by habitat-specific processes (which may be similar to habitat shifts processes), and less sensitive to spatial processes such as habitat selection.

As discussed in chapter 3, the distribution of the different habitats-types in the Mediterranean basin imply that comparing large habitats can be achieved only by the comparisons of very distant localities, like comparing wide *Cystoseira* forests of Corsica and Menorca versus wide shrublands of continental shores. However, such basin-wide study is sensitive to the confounding effect of spatial variations due to other factors than habitats. It makes difficult to answer the question: are *Cystoseira* forests different from shrublands, or rather are islands different from mainlands due to other factors? Hence, with such an approach, it is primordial to sample numerous localities and take care that the different habitat are spatially interspersed as much as possible. In the present work, logistic constraints did not allow to carry out such an important sampling effort. Hence we used a design with habitat-types nested within localities for limiting the possible confounding effects of other factors, despite it implied to compare habitat-types within localities of Corsica and Menorca, where rocky seascapes are dominated by *Cystoseira* forests, and alternate habitat-types, such as barren and turf, cover small to medium areas embedded within *Cystoseira* forests (*i.e.* patch of 30 x 30m²).

Our field inventories evidenced that fish are more diversified and abundant in *Cystoseira brachycarpa* forests compared to adjacent barren and turf. Our tank-experiments suggested that both habitat selection and differential mortality possibly contributed to shape the observed differences between habitat-types. However, the relative contribution of habitat selection *vs* differential mortality (in shaping the observed fish distribution patterns) remains unknown. Consequently, the present work does not allow to assess the impacts of past and present losses of *Cystoseira* forest on fish assemblages.

For explaining this latter affirmation, let's consider an hypothetical locality where the current situation is as follow: both *Cystoseira* forest and barren are present and each covers half of the area, and an hypothetical fish species is more abundant in *Cystoseira* forest than in barren. This situation intends to reproduce our field inventories observations. Then, under two extreme scenarios about the relative contribution of habitat selection *vs* differential mortality in shaping the current fish distribution, let's envisage the consequences for fish of *Cystoseira* forest total disappearance from the locality and replacement by barren (Figure 1):

- Scenario 1, fish do not select preferentially one habitat and the current density and distribution pattern result from increased mortality in barren. If the *Cystoseira* forest shifts into barren, fish will suffer from increased mortality in the whole locality (only barren) and consequences for the fish population density might be dramatic.
- Scenario 2, fish mortality is equivalent in both habitats and the current distribution pattern results from a net immigration into *Cystoseira* forest due to habitat preference. If the *Cystoseira* forest shifts into barren, fish individuals will no longer have choice in habitat and they will be distributed homogenously into the whole locality without reduction in density, since mortality in barren is equivalent to mortality in *Cystoseira* forest. Consequences for the fish population density might be negligible at ecological time scale. However, micro-habitat use and behavioral interactions will be changed. Ultimately this might affect selective pressures and the generation and maintenance of biodiversity.

It is worth noting that these two scenarios do not take into account all factors that may affect the habitat-shift induced changes in mortality and habitat selection of the hypothetical fish species, such as the response to habitat shift of its prey and predators. The consequences enunciated above are therefore certainly inaccurate. They have been mentioned in such a simple way just for the purpose of illustrating how is important to know the relative contribution of habitat selection *vs* differential mortality, when drawing prediction about the role of *Cystoseira* forests from interpretation of current fish distributions patterns (*i.e.* by using a space for time approach).

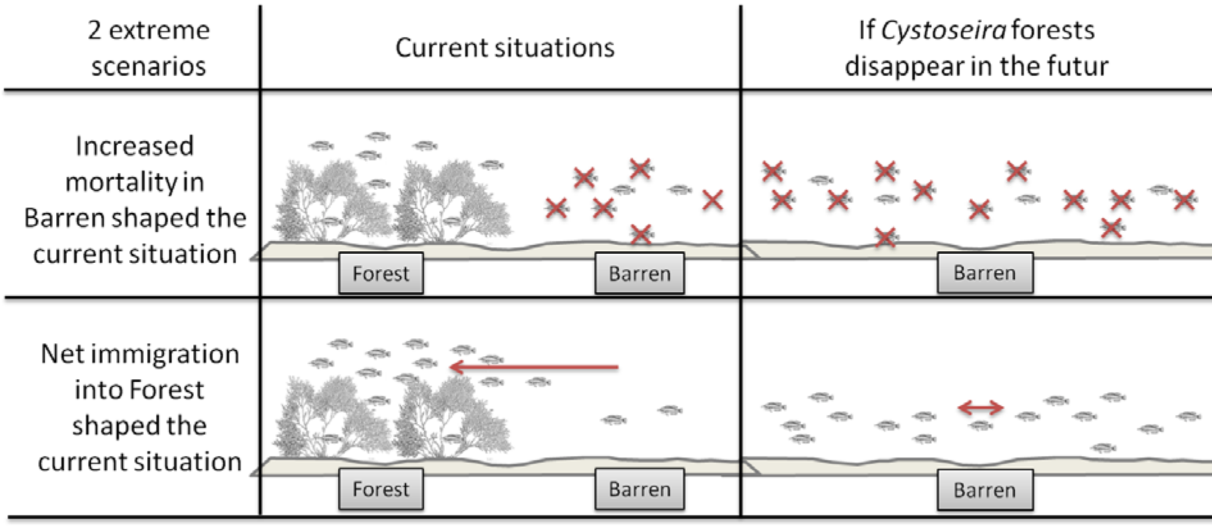


Figure 1: Two extreme scenarios about the relative contribution of habitat selection *vs* differential mortality in shaping the current fish distribution patterns, and their different consequences in case of *Cystoseira* forest total disappearance.

3 Conclusion

Despite the present work does not allow to quantify the impacts of past and present losses of *Cystoseira* forest on fish assemblages, it evidences that coastal fishes better survive in and/or immigrate into *Cystoseira* forests due to the high habitat structural complexity. Hence, *Cystoseira* spp., as 'habitat-former', has a paramount role in mediating lethal and/or behavioral interactions among fish. This emphasizes the need to develop better management practices of the human activities impacting *Cystoseira* spp. and to develop methods (*e.g.* ecological engineering) to restore impacted or lost *Cystoseira* forests (see Gianni *et al.* 2013).

4 Perspectives

To better understand the ecological functions of *Cystoseira* spp. and to foresee consequences of possible further decline of *Cystoseira* forest, further studies should notably: 1) expand the surveys of rocky reefs biodiversity, over broader spatial and temporal scales, 2) investigate more deeply the lethal and behavioral interactions among competitors and between prey and predators, and 3) identify the sources of organic material sustaining the food web of each habitat-type.

For the latter point, we already suggested the combination of carbon, nitrogen and sulfur stable isotopes analyses and the analysis of fatty acid biomarkers. For the two former points, here are few remarks on the possible approaches that could be employed.

4.1 Biodiversity surveys and monitoring

In order to achieve a more global picture of rocky reefs ecosystem structures and functioning, it would be valuable:

- to survey during both day- and night-time, several time during each season, for considering dial, seasonal and other (spatio-)temporal variations of ecosystems structures.
- to survey only wide habitat units for avoiding the importance of small-scale habitat selection and possible edge effects.
- to survey all trophic compartments (including invertebrates, prey of many fish) for better assessing food web structure.
- to use sampling methods adapted at best to life history traits of organisms, including 'Enclosed Anesthetic Station' for sampling crypto-benthic fish.

Moreover, long-term monitoring programs have to be set-up. The lack of time series prevented to clearly assess the consequences of past *Cystoseira* forests losses. Building time series from now would help to detect the soonest as possible the future changes in habitats and their consequences on the associated faunal communities.

4.2 Investigating the ecological processes

To better foresee the consequences of further *Cystoseira* forest regression, it would be valuable to assess the relative contribution of habitat selection *vs* differential mortality in shaping presently-observed fish distribution patterns (Aim 1).

To better identify the factors that affect the relative contribution of habitat selection *vs* differential mortality, it would be valuable to assess the effects of habitat structure, food availability and predation risks (Aim 2).

To achieve Aim 1, experiments must include habitat-specific food and shelter availability, as well habitat-specific competitor and predator assemblages. Because it is almost impossible to reproduce in a tank the natural structure of invertebrate assemblages (fish food), field-based experiments appear the unique alternative. In the field, approaches such as Capture-Mark-Recapture and Sonar Tracking might be suitable. Capture-Mark-Recapture (or Fish tagging and Visual Census) approach is commonly used for assessing growth, mortality and movements of organisms (and possibly their habitat selection) (Chapman & Kramer 2000). Sonar tracking is also very efficient for following movements of organisms (Koeck *et al.* 2013). Although, these approaches are 'correlative' and do not allow to control the putative factors that affect growth, mortality and habitat selection of organisms. They therefore cannot be suitable to achieve Aim 2.

To achieve Aim 2, experiments must consist in an orthogonal design whose treatments are the combinations of absence/presence of each factor: food, shelter, competitor, predator (Horinouchi *et al.* 2013) whose the amount/density must be habitat-specific. This is a challenge for experimentalists. An approach commonly used for comparing between treatments mortality rate (and eventually growth rate) is tethering experiments (Peterson & Black 1994). However, Chapter 4 evidenced that *S. ocellatus* anti-predation behavior consists notably in vertical and horizontal movements within and across the different strata of the vegetated habitats (*e.g.* in *Cystoseira* forest: understory, canopy, open-water). It is highly likely that anti-predation movements of tethered *S. ocellatus* would be more impeded in *Cystoseira* forest than in Dictyotales shrublands, because the leash tying off the prey would get more rapidly tangled around the complex and rigid *Cystoseira* branches than around the simple and fleshly Dictyotales thallus. This expected interaction between the artifact of intervention and the habitat treatment discourage the use of tethering experiment for our study systems (Peterson & Black 1994). Experiments employing cages to exclude predators have also been used for assessing predation mortality. However, cages excluding predators does not prevent migration of prey fish (*e.g.* prey fish immigrate into cages for seeking shelter), which may generate important artifacts (Hindell *et al.* 2000). Hence, cages preventing migration of both prey and predator ('mesocosms') appear a valuable alternative, since it allows to control within the cage every factors. For assessing the factors affecting prey fish habitat selection, 'mesocosms' cages may be derived into choice arena (Figure 2).

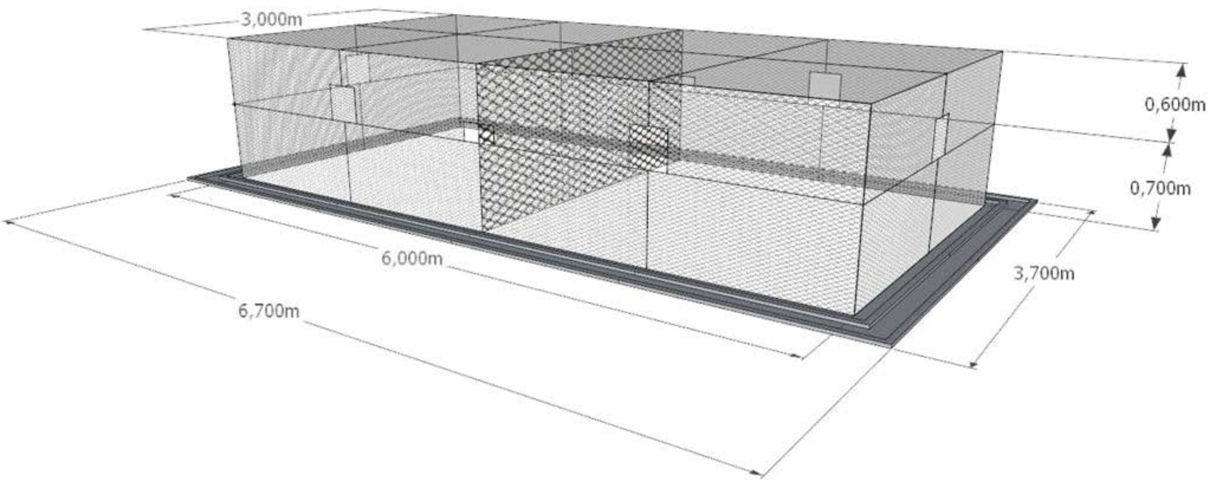


Figure 2. Schema of a choice-arena 'mesocosm' cage enclosing both prey and predator. The cage is composed by two compartments, separated by a mesh size large enough for allowing prey fish to shift compartments, but small enough for preventing predatory fish to shift compartments. This allow to control the absence/habitat-specific presence of predators.

5 References

See references in the french version of this chapter, on page 176.

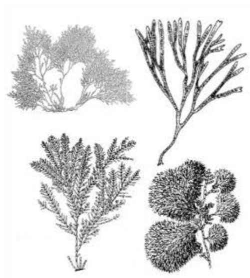
Crédits graphiques

Toutes les figures et les panels de photos ont été conçus par l'auteur de ce manuscrit.

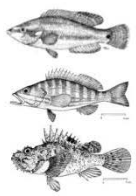
Les photos ont été prises par les personnes suivantes :

- Chapitre 1 - Figure 1 : Pierre THIRIET
- Chapitre 3 - Page de garde : Adrien CHEMINEE
- Chapitre 3 - Photos panel 1: Adrien CHEMINEE
- Chapitre 3 - Photos panel 2 : Pierre THIRIET
- Chapitre 4 - Page de garde : photos de macroalgues, Pierre THIRIET ; photos de poissons, voir incrustations
- Chapitre 5 - Page de garde : a, Gabriel DEVIQUE ; b, Thibault GARNIER ; c, Samuel BRANTHOMME ; d et e, Pierre THIRIET.
- Chapitre 5 - Photos panel 1 : Arnaud ABADIE

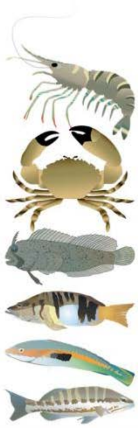
La provenance des icônes qui n'ont pas été créées par l'auteur mais qui ont été utilisées dans certaines figures est présentée ci-dessous:



Fisher W., Schneider M. et Bouchot M.-L. (1987) Fiches FAO d'identification des espèces pour les besoins de la pêche, Méditerranée et Mer Noire, Zone de pêche 37, révision 1, Volume I Végétaux et invertébrés. CEE et FAO, Rome



Fisher W., Schneider M. et Bouchot M.-L. (1987) Fiches FAO d'identification des espèces pour les besoins de la pêche, Méditerranée et Mer Noire, Zone de pêche 37, révision 1, Volume II Vertébrés. CEE et FAO, Rome



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Résumé

Dans l'Infralittoral rocheux méditerranéen, les algues brunes du genre *Cystoseira* forment des habitats structurellement complexes, dénommés forêts à *Cystoseira*. A cause de certaines activités anthropiques, ces forêts ont déjà disparu dans de nombreuses localités et sont en train de régresser dans d'autres. Elles ont été (sont) généralement remplacées par des habitats structurellement moins complexes de type brousse, gazon ou désert.

Cette thèse a visé à estimer les possibles conséquences pour les poissons de la régression des forêts à *Cystoseira* et à identifier les processus écologiques en cause. Plusieurs approches complémentaires ont été employées : inventaires de macroalgues et de poissons, expériences de prédation et de sélection d'habitats en aquarium, analyses de composions isotopiques et de contenus stomacaux.

Les densités de poissons proie et prédateur étaient plus importantes dans les forêts à *Cystoseira* que dans les habitats structurellement moins complexes. Cela peut résulter, au moins en partie, du rôle "refuge" de *Cystoseira* spp. qui induit (1) une plus faible mortalité des poissons proies et prédateurs dans les forêts, due à une plus grande disponibilité en abris et en nourriture, respectivement, (2) une immigration nette des poissons dans les forêts due à leur préférence pour cet habitat structurellement complexe. De plus, *Cystoseira* spp. pourrait être une importante source de matière organique pour l'écosystème. Ce potentiel rôle "trophique" mérite des études complémentaires.

Ce travail suggère que la régression des forêts à *Cystoseira* est néfaste pour les poissons et souligne donc la nécessité de mieux gérer les activités humaines impactant *Cystoseira* spp..

Abstract

In Mediterranean rocky subtidal, large brown algae belonging to the genus *Cystoseira* form structurally complex habitats, called *Cystoseira* forest. Due to anthropogenic stressors, *Cystoseira* forests disappeared from numerous localities in the Mediterranean Sea and are deteriorating in other localities. *Cystoseira* forests are usually replaced by structurally less complex habitats, such as shrublands, turfs and barrens.

This PhD aimed to assess putative consequences for fish of *Cystoseira* forest degradation, and to identify the underlying ecological processes. Multiple complementary approaches were used: macroalgae and fish field surveys, tank-based predation and habitat-choice experiments, stable isotopes and stomach contents analyses.

Densities of prey and predatory fish were higher in *Cystoseira* forests compared to structurally less complex habitats. This may be due to the shelter role of *Cystoseira* spp. that induces (1) reduced mortality of prey and predatory fish in forests, due to high shelter and food availability, respectively, and (2) net immigration of fish into forests due to their preference for this structurally complex habitat. Moreover, *Cystoseira* spp. may be an important source of organic matter to the ecosystem. This possible trophic role deserves complementary studies.

This work suggests that *Cystoseira* forest degradation are harmful to fish and from this perspective stresses the need to better manage human activities impacting *Cystoseira* spp..